A REVISION OF THE DIDELPHID MARSUPIAL GENUS *MARMOSOPS*, PART 1. SPECIES OF THE SUBGENUS *SCIOPHANES*

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ABSTRACT

In this report, the first installment of a comprehensive revision of the didelphid marsupial genus *Marmosops*, we revise the species of the subgenus *Sciophanes*. Based on morphological character variation among almost 300 examined specimens—which we interpret in the context of a previously published analysis of molecular sequence data—this revision recognizes 12 valid species in three monophyletic species groups: the Parvidens Group (including *M. pakaraimae*, *M. parvidens*, and *M. pinheiroi*), the Fuscatus Group (*M. carri*, *M. fuscatus*, *M. handleyi*, and *M. invictus*), and the Bishopi Group (*M. bishopi*, *M. juninensis*, *M. ojastii*, and two new species). For each species we summarize information about type material, ecogeographic distribution, and diagnostic morphological characters. Despite our diligent search for relevant material in North and South American museums, the absence of any specimens of *Sciophanes* from vast Amazonian and Andean landscapes with seemingly suitable habitat suggests that significant range extensions and/or new species will result from future inventory fieldwork.

INTRODUCTION

Members of the genus *Marmosops* are small (<200 g) didelphid marsupials that collectively range from eastern Panama to southern Bolivia and southeastern Brazil. Black-masked, long-tailed, and pouchless, they were classified for many years in the genus *Marmosa* along with other superficially similar taxa (e.g., by Tate, 1933; Cabrera, 1958). However, subsequent morphological and molecular research (reviewed by Voss et al., 2004; Voss and Jansa, 2003) has shown that the species referred to *Marmosops* by Matschie (1916), together with those later referred to the genus by Gardner and Creighton (1989), form a strongly supported monophyletic group that is not closely related to *Marmosa* (sensu stricto). Instead, *Marmosops* is now placed in the didelphine tribe Thylamyini, a clade that also includes *Chacodelphys*, *Cryptonanus*, *Gracilinanus*, *Lestodelphys*, and *Thylamys* (Voss and Jansa, 2009).

Unlike most other thylamyines, which occur in dry forests, savannas, grasslands, and high-latitude deserts, species of *Marmosops* typically inhabit humid-forest habitats. In particular, the genus is widespread—perhaps ubiquitous—in cis-Andean lowland rain forests (Mustrangi and Patton, 1997; Patton et al., 2000; Voss et al., 2001), and it also occurs in premontane and montane rain forests of the Andes, the Venezuelan coastal cordilleras, and Pantepui (Díaz-N. et al., 2011; Voss et al., 2013; García et al., 2014). Insofar as known, these are scansorial opossums that are primarily active on the ground and within a few meters of the ground in understory vegetation (Malcolm, 1991; Patton et al., 2000; Voss et al., 2001; Cunha and Vieira, 2002; Vieira and Monteirho-Filho, 2003; Loretto and Vieira, 2008), where they apparently forage for arthropods (mostly insects) and fruit (Passamani, 1995; Leiner and Silva, 2007; Lessa and Costa, 2010). At least in the Atlantic Forest of southeastern Brazil, species of *Marmosops* appear to be semelparous breeders that experience almost complete postreproductive mortality, such that successive adult generations are nonoverlapping (Lorini et al., 1994; Leiner et al., 2008).

The genus as a whole has never been revised, although taxonomic analyses of specimens collected in the course of regional faunal surveys have contributed numerous insights (Mustrangi and Patton, 1997; Voss et al., 2001, 2004, 2013; Díaz-Nieto et al., 2011; García et al., 2014). The current classification formally recognizes 17 valid species of *Marmosops*, a total that includes the 15 species recognized by Gardner and Creighton (2008) and two others subsequently described as new (Voss et al., 2013; García et al., 2014). Among

other didelphid genera, only *Monodelphis* (with 22 currently recognized species; Pavan et al., 2014; Pavan, 2015) and *Marmosa* (with 19 species; Voss et al., 2014) are comparably diverse.

Although molecular sequence data have been analyzed in a few taxonomic studies of *Marmosops* (e.g., by Mustrangi and Patton, 1997; Patton et al., 2000; Voss et al., 2004, 2013), much of the current nomenclature is based exclusively on phenotypic comparisons. Unfortunately, the morphology-based primary taxonomic literature is inadequate to confidently identify several species, secondary sources (e.g., field guides and keys) that are routinely consulted for identification purposes are sometimes unreliable, and some currently accepted synonymies are not based on firsthand examination of type material. Not surprisingly, museum specimens of *Marmosops* are often misidentified.

This report, the first installment of a comprehensive generic revision, is based on a multiyear study of morphological specimens (including all relevant type material), the results of which we interpret in the context of a recently completed analysis of molecular sequence data (Díaz-Nieto et al., 2016a). Among the more robustly supported outcomes of that analysis was the discovery of a basal dichotomy in the genus, resulting in two clades that were formally recognized as subgenera. This report concerns the subgenus *Sciophanes*, which contains *Marmosops parvidens* (the type species), and 11 additional species, including two new species.

Materials and Methods

Specimens: The morphological specimens we examined and others mentioned below are preserved in the following collections (listed in order of their standard institutional abbreviations): AMNH (American Museum of Natural History, New York), BMNH (Natural History Museum, London), CM (Carnegie Museum, Pittsburgh), CTUA (Colección Teriológica de la Universidad de Antioquia, Medellín), EPN (Escuela Politécnica Nacional, Ciencias Biológicas, Quito), FMNH (Field Museum, Chicago), ICN (Colección de Mamíferos Alberto Cadena García, Instituto de Ciencias Naturales, Bogotá), INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus), ISEM (Institut des Sciences de l'Evolution de Montpellier, Montpellier), KU (University of Kansas Biodiversity Research Center, Lawrence), LACM (Los Angeles County Museum, Los Angeles), LSUMZ (Louisiana State University Museum of Zoology, Baton Rouge), MHNUC (Museo de Historia Natural, Universidad de Caldas, Manizales), MSB (Museum of Southwestern Biology, University of New Mexico, Albuquerque), MUSM (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima), MVZ (Museum of Vertebrate Zoology, University of California, Berkeley), QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito), ROM (Royal Ontario Museum, Toronto), UF (Florida Museum of Natural History, University of Florida, Gainesville), UMMZ (University of Michigan Museum of Zoology, Ann Arbor), and USNM (National Museum of Natural History, Washington).

Measurements: We transcribed total length (nose to fleshy tail tip, TL) and length of tail (basal flexure to fleshy tip, LT) from specimen labels, and we computed head-and-body length (HBL) by subtracting LT from TL. We also transcribed length of hind foot (heel to tip of longest claw, HF), length of ear (from notch, Ear), and weight from specimen labels or field notes, but we sometimes remeasured HF on fluid-preserved specimens to check the accuracy of values recorded by the collector, and we used our values whenever large discrepancies were found. (In a few instances we omitted problematic collectors' measurements when computing sample means and observed ranges.) All external measurements are reported to the nearest millimeter (mm), and all weights are reported to the nearest gram (g).

Craniodental measurements were taken with digital calipers as skulls were viewed under low (6–12×) magnification. Measure-

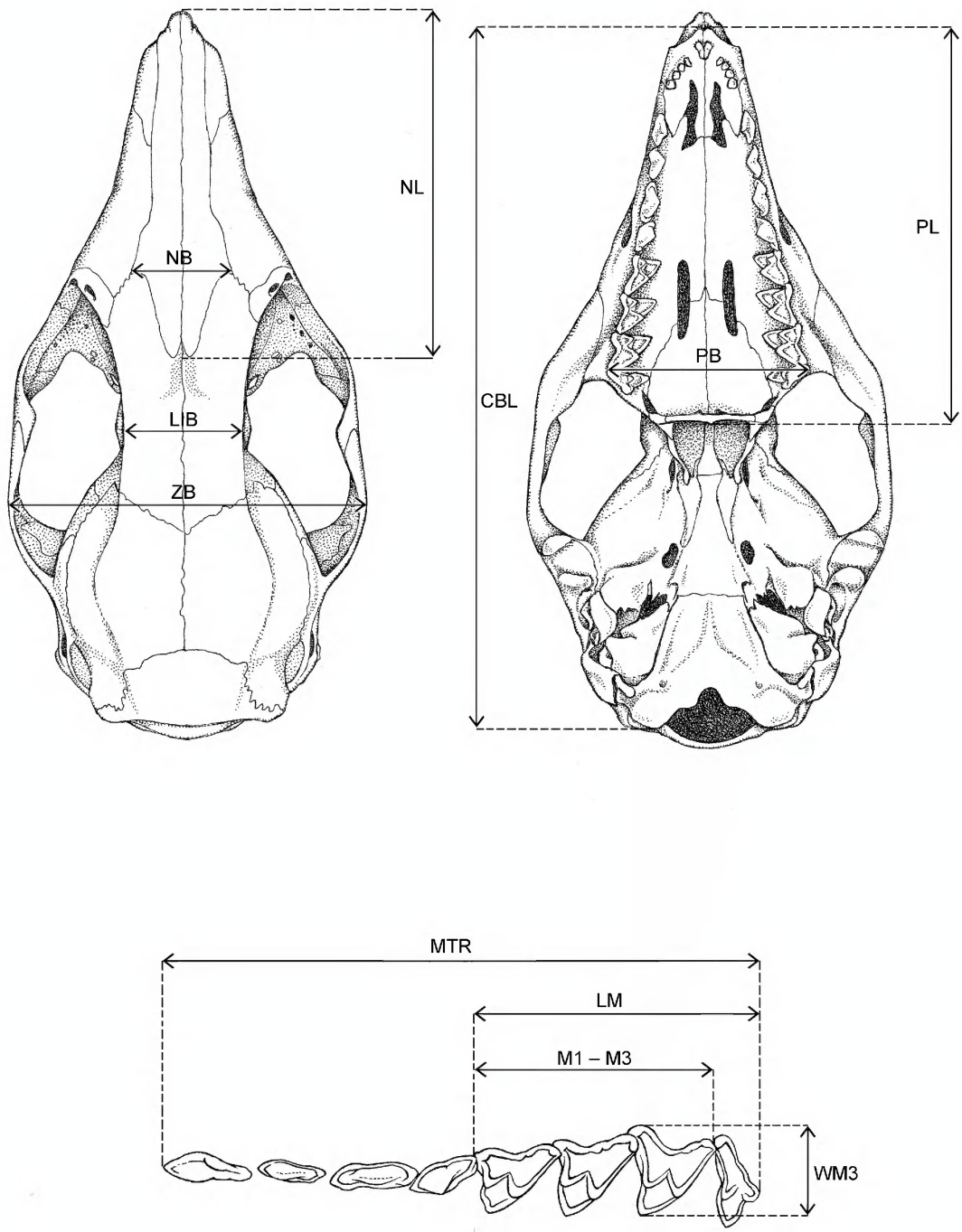

FIG. 1. Dorsal and ventral cranial views and occlusal view of the maxillary dentition of *Marmosops pinheiroi*, showing the anatomical limits of 11 craniodental measurements defined in the text.

ment values were recorded to the nearest 0.01 mm, but those reported herein are rounded to the nearest 0.1 mm. The following dimensions were measured (fig. 1):

Condylo-basal length (CBL): measured from the occipital condyles to the anteriormost point of the premaxillae.

Nasal length (NL): the greatest anteroposterior dimension of either bone.

Nasal breadth (NB): measured between the triple-point sutures of the nasal, frontal, and maxillary bones on each side.

Least interorbital breadth (LIB): measured at the narrowest point across the frontals between the orbits, even when the postorbital constriction (between the temporal fossae) is narrower.

Zygomatic breadth (ZB): measured at the widest point across both zygomatic arches.

Palatal length (PL): measured from the anteriormost point of the premaxillae to the postpalatine torus, including the postpalatine spine (if present).

Palatal breadth (PB): measured across the labial margins of the M4 crowns, at or near the stylar A position.

Maxillary toothrow length (MTR): measured from the anterior margin of C1 to the posterior margin of M4.

Length of molars (LM): measured from the anteriormost labial margin of M1 to the posteriormost point on M4.

Length of M1–M3 (M1–M3): measured from the anteriormost labial margin of M1 to the posteriormost point on M3.

Width of M3 (WM3): measured from the labial margin of the crown at or near the stylar A position to the lingual apex of the protocone.

Age criteria: Unless otherwise noted below, we recorded measurements and scored qualitative morphological data from adult specimens only. Following Voss et al. (2001), a specimen was judged to be juvenile if dP3 was still in place; subadult if dP3 had been shed but P3 was still incompletely erupted; and adult if the permanent upper dentition (I1–I5, C1, P1–P3, M1–M4) was complete. Because dP3 is molariform, juvenile specimens have only two premolariform teeth (P1 and P2) between the upper canine and the first molariform tooth (dP3), whereas adults have three fully erupted premolariform teeth (P1, P2, and P3) between the upper canine and the first molariform tooth (M1).

COMPARATIVE MORPHOLOGY

Species of *Marmosops* can be distinguished from one another by qualitative differences in numerous characters of the integument, skull, and dentition. We describe and illustrate these characters in the accounts that follow, using anatomical terminology defined or referenced by Voss and Jansa (2003, 2009) and Díaz-N. et al. (2011). For the most part, our usage is consistent with morphological descriptors defined by Brown (1971), Brown and Yalden (1973), Bown and Kraus (1979), and Wible (2003), which should be consulted for relevant explanations and illustrations.

Integument

Dorsal pelage color: As in many other groups of small nocturnal mammals, dorsal pelage color exhibits a limited range of variation among species of *Marmosops*. In general, the species treated in this report are soberly colored in various dull, substrate-matching shades of brown, but coat-color contrasts are sometimes striking (fig. 2). Ordinary color descriptors (e.g., "pale grayish brown") are sufficient for most comparative purposes, but we also cite Ridgway's (1912) terminology, which is always capitalized (e.g., Dark Umber).

Ventral pelage color and pattern: Ventral pelage hairs can be the same color from base to tip, or they can be grayish basally with paler tips. Ventral fur composed of hairs that are the same color from base to tip is said to be self-colored (e.g., self-white, self-buffy, etc.; Tate, 1933), whereas ventral fur composed of hairs

FIG. 2. *Marmosops handleyi* (**above**; photographed by J. Díaz-Nieto at Finca Costa Rica, Antioquia, Colombia) and *M. parvidens* (**below**; photographed by T. Semedo near Urucará, Amazonas, Brazil). In addition to obvious differences in body pelage color, these species differ in forefoot markings: whereas *M. handleyi* has dark metacarpal fur that contrasts with the pale fur of the manual digits, *M. parvidens* has all-pale forefeet.

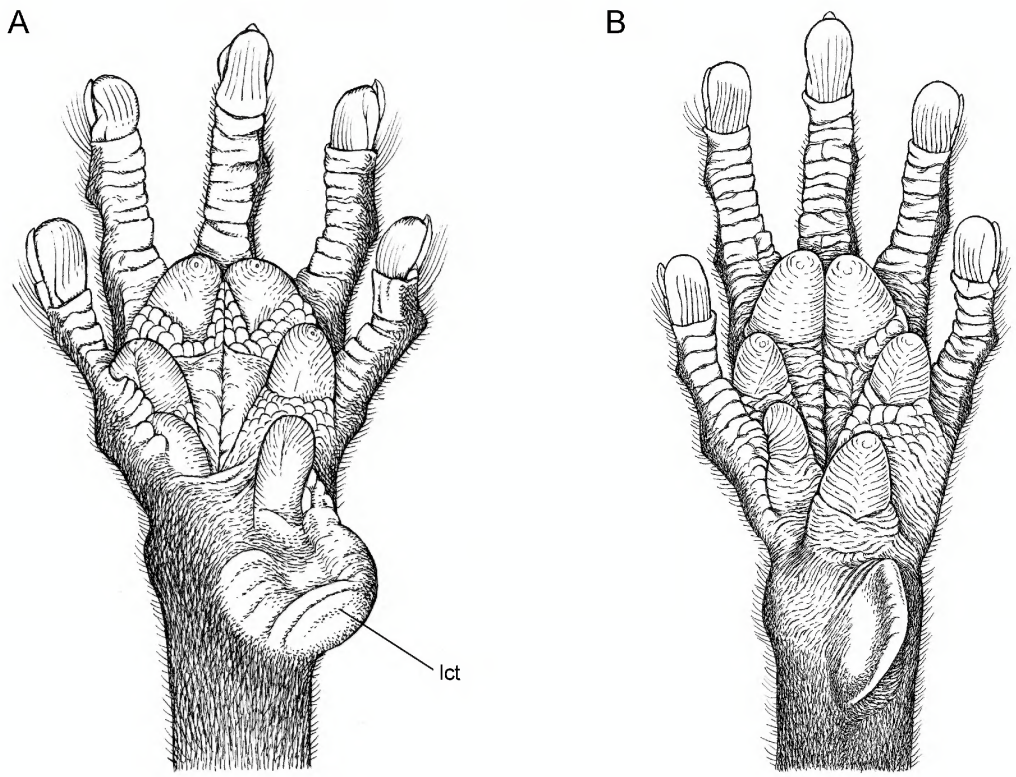

FIG. 3. Plantar views of left forefoot (manus) and wrist of *Marmosops pinheiroi* (**A**, AMNH 267346) and *M. bishopi* (**B**, MUSM 23801) illustrating different morphologies of the lateral carpal tubercle (**lct**), which is spoon shaped in adult males of *M. pinheiroi* and bladelike (laterally compressed) in adult males of *M. bishopi*.

with gray bases is said to be gray based. In general, the fur of the chin (including the oral margins), and groin (including the scrotum) is self-whitish in *Marmosops*, but the coloration of the throat, chest, abdomen, and the inside surfaces of the fore- and hind limbs is taxonomically variable. In several species of the subgenus *Sciophanes*, the entire ventrum (except the chin and groin) is covered with gray-based fur, but in other species there is a continuous midventral zone of self-colored fur that extends from the chin to the groin. In some species the self-whitish midventral fur is much narrowed by lateral zones of gray-based fur, and in others the self-colored fur is reduced to a discontinuous midventral streak. The short fur surrounding the mammae of lactating adult females is sometimes reddish or brownish; within the subgenus *Sciophanes* we observed this trait in specimens of *M. bishopi* (e.g., TTU 101238), *M. chucha* (FMNH 69837), *M. magdalenae* (ICN 19924), and *M. pinheiroi* (USNM 393529).

Gular gland: Many species in the nominotypical subgenus of *Marmosops* have a conspicuous midventral patch of naked skin on the throat that is presumably homologous with the gular gland of other didelphids (Barnes, 1977), but species of the subgenus *Sciophanes* lack any external trace of glandular activity in the throat region, which is uniformly furred and unstained by cutaneous secretions.

Dorsal pelage of manus and pes: The dorsal surface of the manus is covered with short hairs that are uniformly pale in some species, whose forefeet lack any pigmental contrast between the metacarpal and digital pelage. In other species, however, the metacarpals are covered with dark (brownish or grayish) hairs that

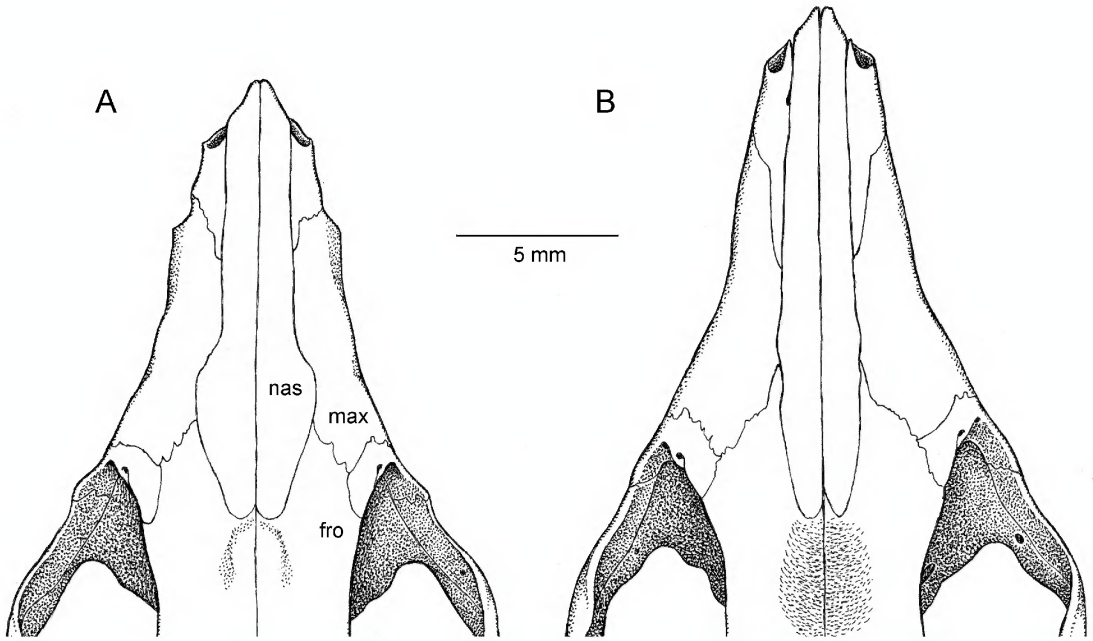

FIG. 4. Dorsal views of the rostrum of *Marmosops invictus* (**A,** USNM 306386) and *M. fuscatus* (**B,** FMNH 22174), illustrating taxonomic differences in nasal width. Abbreviations: **fro,** frontal; **max,** maxillary; **nas,** nasal.

contrast abruptly in color with the paler digital fur. (See fig. 2 for contrasting examples of manual pelage markings.) Hind feet exhibit similar variation in the nominotypical subgenus of *Marmosops*, some species of which have dark metatarsals that contrast with abruptly paler digits, but all species of the subgenus *Sciophanes* have uniformly pale-furred hind feet.

Carpal tubercles: Prominent carpal tubercles that are supported internally by the pisiform bone (Lunde and Schutt, 1999; Voss et al., 2001: fig. 20) are present on the lateral surface of the wrist of adult males of most species of *Marmosops*, but these are sexually dimorphic structures that do not occur in females, and they are often not apparent on the wrists of immature males. In the subgenus *Sciophanes*, carpal tubercles are taxonomically variable in shape. In some species they are spoon shaped (broadly concave anteriorly; fig. 3A), whereas in others they are blade-like (laterally flattened and aligned with the long axis of the wrist; fig. 3B).

Antebrachial vibrissae: Most didelphids, including most species of the nominotypical subgenus of *Marmosops*, have a single long vibrissa on the dorsolateral surface of the forearm, but species of the subgenus *Sciophanes* consistently have two antebrachial vibrissae (Díaz-N. et al., 2011: fig. 5). The only exceptional species known to us is *M.* (*M.*) *ocellatus*, of which most examined specimens appear to have two antebrachial vibrissae.

Mammae: Didelphid mammae are typically restricted to the inguinal or abdominal region, where they form a roughly circular array that often includes an unpaired median teat (Voss and Jansa, 2009: fig. 5b). We summarize mammary morphology as teat counts using the formula R–M–L = T (Right–Median–Left = Total). Thus, a species with three teats on the right side, one unpaired median teat, and three teats on the left side would have a mammary formula of 3–1–3 = 7. In species with nine or fewer teats, all of the mammae are circularly arranged and abdominal-inguinal, but in species with 11 or more mammae—for example, *Marmosops (Marmosops) ocellatus*, with mammary formula 6–1–6 = 13 (Voss et al., 2004)—one or more pairs are

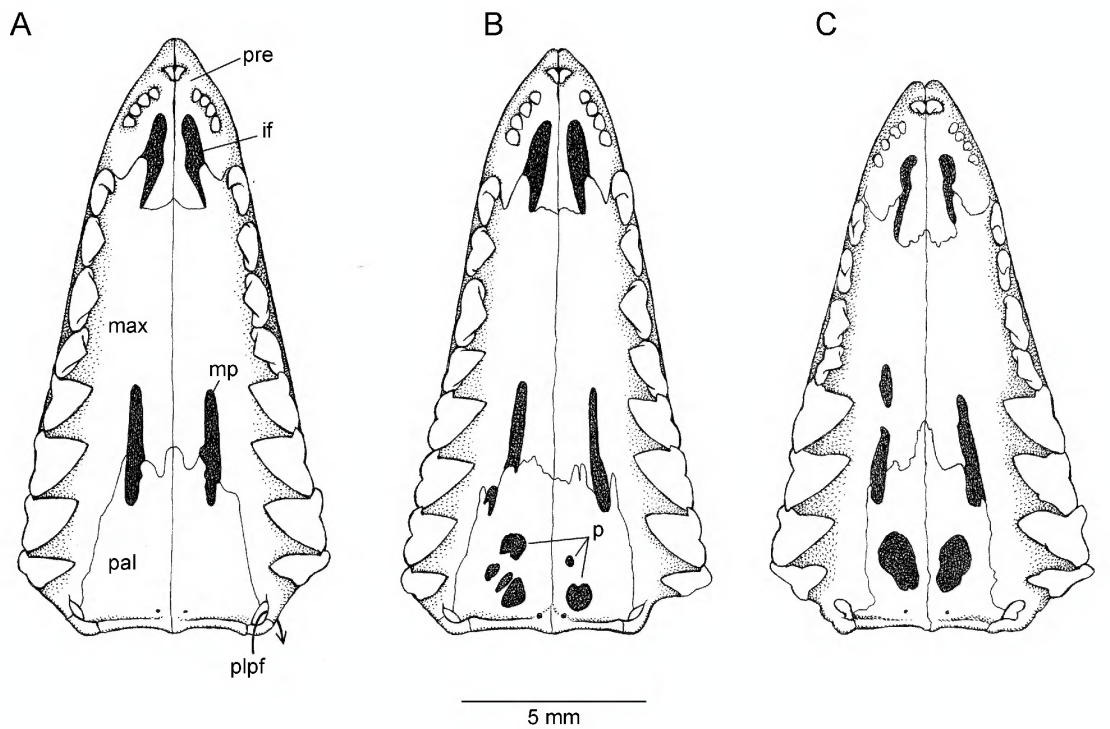

FIG. 5. Ventral views of the palates of *Marmosops parvidens* (**A,** AMNH 267359), *M. juninensis* (**B,** AMNH 230016), and *M. magdalenae* (**C,** ICN 19926) illustrating species differences in the presence, absence, and morphology of palatal fenestrae and foramina. Abbreviations: **if,** incisive foramen; **max,** maxillary bone; **mp,** maxillopalatine fenestra; **p,** palatine fenestrae; **pal,** palatine bone; **plpf,** posterolateral palatine foramen; **pre,** premaxillary bone.

said to be "pectoral" (Tate, 1933) because they are positioned anterior to the circular abdominal-inguinal array, although none that we have seen actually occur on the chest. Insofar as known, species in the subgenus *Sciophanes* have no more than nine mammae, all of which are abdominal-inguinal.

Caudal coloration: The tail in *Marmosops* is furred only at the base and appears to be completely naked because the three bristlelike hairs emerging from each scale are visible only under magnification. Some species have unicolored tails that are dark from base to tip on both dorsal and ventral surfaces, but in other species the caudal integument is more heavily pigmented dorsally and/or basally than it is ventrally and/or distally. Tails that are distinctly darker dorsally than ventrally are said to be *bicolored*, whereas tails that are darker basally and paler near the tip are said to be *particolored*. No species of the subgenus *Sciophanes* has a distinctly particolored tail.

Skull

Nasal shape: The paired nasal bones are narrow and parallel sided anteriorly, but in most species of *Marmosops* they are much wider posteriorly than anteriorly because they are laterally expanded at or near the frontal-maxillary suture (fig. 4A). However, in some species of the nominotypical subgenus (e.g., *M. incanus*) and in two species of *Sciophanes* (namely *M. carri* and *M. fuscatus*), the nasals are almost as narrow posteriorly as they are anteriorly, with only slight lateral expansion near the frontal-maxillary suture (fig. 4B).

Lacrimal foramina: The lacrimal foramina transmit the lacrimal canaliculi and a small

accompanying vein through the lacrimal bone, which forms the anterodorsal margin of the didelphid orbital fossa (Wible, 2003). Most species of *Marmosops* have two lacrimal foramina on each side, but the position of these openings is taxonomically variable. In some species of *Sciophanes* the foramina (or foramen, when only one is present) are more or less concealed from lateral view inside the anterior orbital margin (fig. 14A), but in others they are laterally exposed anterior to the orbit (fig. 14B). Yet other species exhibit an intermediate morphology in which one foramen (usually the dorsalmost) is completely or partially concealed inside the orbit and the other (usually the ventralmost) is exposed on the orbital margin, and this character is sometimes quite variable even in local populations.

Squamosal-jugal overlap: The zygomatic process of the squamosal is more or less acutely pointed and broadly overlapped dorsally by the jugal in most species of *Marmosops* (fig. 23A). But in *M.* (*Sciophanes*) *juninensis* the squamosal zygomatic process is rounded and not dorsally overlapped by the jugal, or is only shallowly overlapped by that bone (fig. 23B).

Subsquamosal foramen: The subsquamosal foramen[1] is a lateral opening in the squamosal bone that exposes the underlying petrosal just dorsal to the ear region of many marsupials. In the subgenus *Sciophanes* the subquamosal foramen is anteroposteriorly elongated, revealing not only the sulcus for the prootic sinus, but also a substantial strip of the relatively featureless lateral surface of the pars canalicularis behind that groove (fig. 9A). By contrast, the subsquamosal foramen in the nominotypical subgenus is shorter and does not extend posteriorly much behind the sulcus for the prootic sinus (fig. 9B).

Palatine fenestrae: The didelphid bony palate is perforated by several pairs of foramina

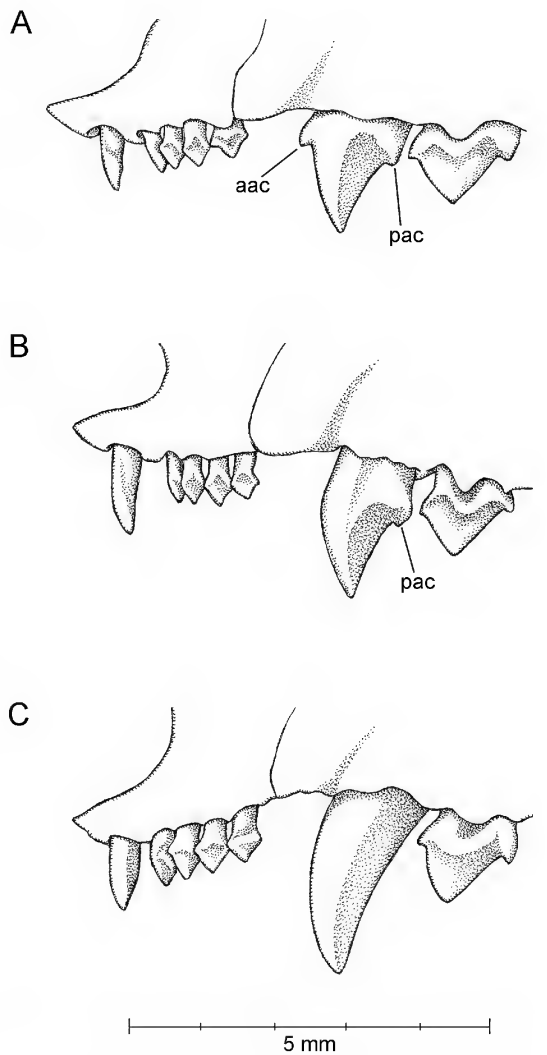

FIG. 6. Lateral view of anterior left upper dentition (I1–P1) of *Marmosops pinheiroi* (**A,** AMNH 267349), *M. magdalenae* (**B,** ICN 18788), and *M. carri* (**C,** KU 120254) illustrating species differences in the presence or absence of accessory upper canine (C1) cusps. All illustrated specimens are males. Abbreviations: **aac,** anterior accessory cusp; **pac,** posterior accessory cusp.

[1] Our use of the term "subsquamosal foramen" is consistent with its original definition (Cope, 1880) and with well-established anatomical usage in the marsupial literature (e.g., Gregory, 1910; Archer, 1976), but Wible (2003: 183) referred to this opening as the "suprameatal foramen," a neologism.

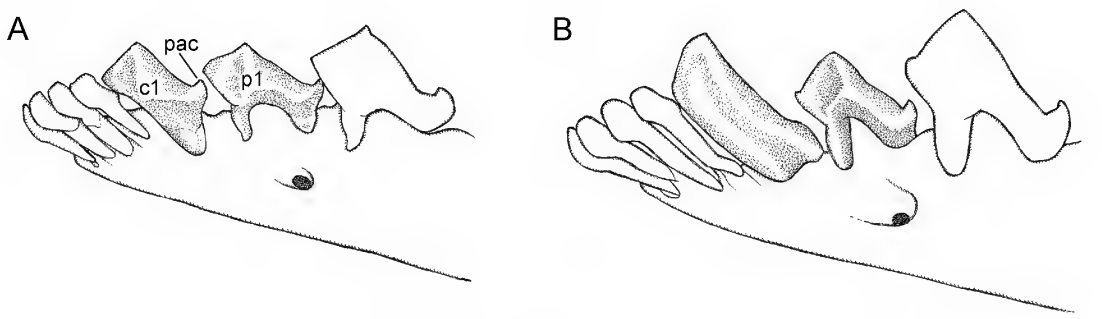

FIG. 7. Lateral view of anterior left lower dentition of *Marmosops parvidens* (**A,** AMNH 266425) and *M. carri* (**B,** KU 120254) illustrating species differences in lower canine (**c1**) morphology. In *M. parvidens*, c1 is subequal in height with the first lower premolar (**p1**), and it has a distinct posterior accessory cusp (**pac**). By contrast, c1 in *M. carri* is distinctly taller than p1 and lacks a posterior accessory cusp. Both illustrated specimens are males.

(transmitting ducts, nerves, and/or blood vessels) and fenestrae (which do not transmit anything), some of which exhibit important taxonomic variation (fig. 5). All didelphids have incisive foramina, which occupy the premaxillary-maxillary suture and transmit the nasopalatine ducts between the oral and nasal cavities. In most species of *Marmosops* the incisive foramina extend posteriorly only between the upper canines, but in at least one species of the nominotypical subgenus they are much longer, extending posteriorly between the first upper premolars (Mustrangi and Patton, 1997: fig. 15). Most didelphids also have maxillopalatine fenestrae and posterolateral palatal foramina, both of which are in the maxillary-palatine suture, but these openings are not known to exhibit noteworthy variation among species of *Marmosops*. Instead, the presence or absence of palatine fenestrae—which penetrate the palatine bone just behind the maxillopalatine fenestrae—is a diagnostically useful character for species recognition in both subgenera.

Some species of the subgenus *Sciophanes* have completely ossified palatines that lack any trace of fenestration (fig. 5A), whereas others have large palatine fenestrae. In some species the palatine fenestrae may consist of multiple irregular openings on each side (fig. 5B), whereas other species may have a single large palatine fenestra on each side (fig. 5C). Although palatine fenestrae sometimes vary in number, shape, and size among conspecific individuals, they tend to be consistently present or consistently absent in most species. Unfortunately, the thin bone of the posterior palate is often damaged by careless specimen preparation, so it is sometimes impossible to determine whether palatine fenestrae were present or absent.

Ethmoid foramen: The didelphid ethmoid foramen is a small perforation in the medial wall of the orbit that transmits the ophthalmic artery and the ethmoidal nerve through the suture between the frontal and orbitosphenoid bones (Wible, 2003). In some species of the subgenus *Sciophanes* the dorsolateral margin of the foramen is consistently formed by the orbitosphenoid, whereas in others it seems to be consistently formed by the frontal. We have not surveyed variation in this character among species of the nominotypical subgenus.

Dentition

C1 accessory cusps: The upper canine (C1) is conventionally caniniform—a simple, recurved, unicuspid tooth—in most marsupials, including all species in the nominotypical subgenus of *Marmosops*. By contrast, the subgenus *Sciophanes* is richly endowed with unusual upper-canine phenotypes, including sexual dimorphism. In both sexes of three species of

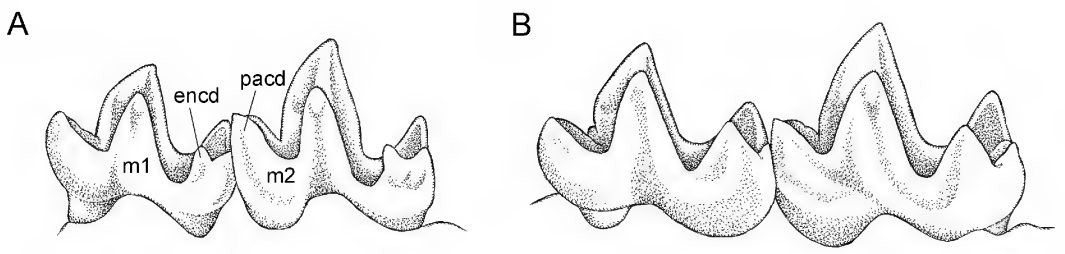

FIG. 8. Lingual view of the first two lower right molars (**m1** and **m2**) of *Marmosops bishopi* (**A,** AMNH 276697) and *M. carri* (**B,** AMNH 234953) illustrating taxonomic differences in the cusp height. In *M. bishopi* the entoconid (**encd**) of m1 is shorter than the adjacent paraconid (**pacd**) of m2, whereas these cusps are subequal in height in *M. carri*.

Sciophanes, C1 is short and provided with both anterior and posterior accessory cusps (fig. 6A), resulting in a strikingly premolariform tooth. In other species of *Sciophanes*, however, females have both anterior and posterior C1 accessory cusps, whereas males have only a posterior accessory cusp (fig. 6B). In some species, both males and females usually have only posterior accessory C1 cusps; and in two species, females usually have only posterior C1 accessory cusps, whereas males have unicuspid teeth (fig. 6C).

As noted previously (Voss and Jansa, 2009: 48), some care is needed in determining C1 crown morphology because accessory cusps are sometimes obliterated by wear, and because false posterior accessory cusps are sometimes created when the trailing edge of C1 is notched by occlusion with p1. Therefore, C1 morphology is best determined from subadult or young adult specimens.

M3 ANTERIOR CINGULUM: A continuous shelf along the anterior (mesial) border of the upper molars in some didelphid species is formed by the union of the anterolabial cingulum with the preprotocrista; in other didelphids, the anterior cingulum is incomplete because the preprotocrista terminates at the base of the paracone (Voss and Jansa, 2003: fig. 13; Voss and Jansa, 2009: 52–54). Both conditions are seen in the genus *Marmosops*, but a complete anterior cingulum, when present, is never very wide in the subgenus *Sciophanes*, and careful examination of unworn teeth under relatively high magnification and good lighting is sometimes necessary to determine this character. Because this character sometimes varies along the toothrow, we scored it from the third upper molar (M3).

LOWER CANINE MORPHOLOGY: Like C1, the lower canine (c1) is conventionally caniniform—a simple, recurved, more or less erect, unicuspid tooth—in most didelphids, including some species in the nominotypical subgenus of *Marmosops*. By contrast, in most species of the subgenus *Sciophanes* c1 is strikingly premolariform: procumbent, subequal in height to the first lower premolar (p1), and with a distinct posterior accessory cusp (fig. 7A). In two species of *Sciophanes*, however, c1 is distinctly taller than p1 and lacks a distinct posterior accessory cusp (fig. 7B).

In addition to the posterior accessory cusp described above, a distinct lingual accessory cusp is present on c1 in *Marmosops* (*Sciophanes*) *handleyi* (see Díaz-N. et al., 2011: fig. 9B). However, this unusual structure occurs polymorphically in other species of *Sciophanes*, and it is sometimes difficult to decide whether it is present or absent in older specimens with worn canines.

RELATIVE HEIGHTS OF M1 ENTOCONID AND M2 PARACONID: The lower first molar (m1) entoconid is conspicuously shorter than the immediately adjacent m2 paraconid in some species of the subgenus *Sciophanes* (fig. 8A), but in other species these cusps are subequal in height (fig. 8B). We have not surveyed this trait among members of the nominotypical subgenus of *Marmosops*, or among other didelphid taxa.

Talonid on m4: In most didelphids the talonid of each lower molar is provided with three cusps (hypoconid, entoconid, and hypoconulid), but in some species of *Sciophanes* the talonid of m4 is bicuspid, apparently because the entoconid and hypoconulid are not distinguishable as separate cusps.

TAXONOMY

Genus *Marmosops* Matschie, 1916

Type species: *Marmosops incanus* (Lund, 1840) by original designation.

Contents: At least 19 species (as recognized by Voss and Jansa, 2009; Voss et al., 2013; Díaz-Nieto et al., 2016a; and this report) in two subgenera.

Description:[2] Combined length of adult head and body ca. 90–195 mm; adult weight ca. 20–140 g. Rhinarium with two ventrolateral grooves on each side of median sulcus; dark circumocular mask present; pale supraocular spot absent; dark midrostral stripe absent; throat gland consistently present in adult males of some species (e.g., *M. incanus*, *M. noctivagus*) but apparently absent in others (e.g., *M. caucae*, *M. parvidens*). Dorsal pelage unpatterned, usually some shade of dull grayish brown, but distinctly redder or grayer in some species; dorsal hair bases always dark gray; dorsal guard hairs short and inconspicuous; ventral fur self-colored (whitish, buffy, or brown) or entirely or partially gray based. Manus mesaxonic (dIII > dIV); manual claws small, shorter than fleshy apical pads of digits; dermatoglyph-bearing manual plantar pads present; central palmar epithelium smooth or sparsely tuberculate; lateral carpal tubercles externally conspicuous on wrists of large adult males of most species; medial carpal tubercles absent in both sexes. Pedal digits unwebbed; dIV longer than other pedal digits; plantar surface of heel macroscopically naked (a microscopic pelage of very short hairs, not coarse fur, is usually present). Pouch absent; mammae varying among examined species from 3–1–3 = 7 to 7–1–7 = 15 (anteriormost pairs "pectoral" when mammae ≥ 11; e.g., in *M. ocellatus*); cloaca present. Tail longer than combined length of head and body, slender and muscular (not incrassate), and macroscopically naked (without a conspicuously furred base); naked caudal integument uniformly dark (usually grayish), bicolored (dark above, pale below), or particolored (dark proximally, paler distally); caudal scales in spiral series, each scale with three bristlelike hairs emerging from caudal margin; median hair of each caudal-scale triplet usually much thicker and darker than lateral hairs; ventral caudal surface modified for prehension distally (with naked median groove and apical pad bearing dermatoglyphs).

Premaxillary rostral process long and well developed in some species (e.g., *M. parvidens*, *M. pinheiroi*) but short in others (e.g., *M. noctivagus*) and apparently absent in some (*M. incanus*). Nasals long, extending anteriorly beyond I1 (concealing nasal orifice in dorsal view), and conspicuously widened posteriorly near maxillary-frontal suture except in *M. carri*, *M. fuscatus*, and *M. incanus* (which have narrow, more or less parallel-sided nasals). Maxillary turbinals (viewed through nasal orifice) elaborately branched. Lacrimal foramina usually two on each side, concealed from lateral view inside orbit (e.g., in *M. parvidens*) or exposed on orbital margin (e.g., in *M. pinheiroi*). Interorbital region without abrupt constrictions; supraorbital margins rounded in some species (e.g., *M. parvidens*), beaded in others (e.g., *M. noctivagus*); postorbital processes usually absent. Left and right frontals and parietals separated by persistent median sutures. Parietal and alisphenoid in contact on lateral braincase (no frontal-squamosal contact). Sagittal crest absent. Petrosal consistently exposed laterally through fenestra in parietal-squamosal suture in most species (but fenestra polymorphically absent in *M. incanus* and *M. noctivagus*). Parietal-mastoid contact present (interparietal does not contact squamosal).

Maxillopalatine fenestrae present; palatine fenestrae present in some species (e.g., *M.*

[2] After Voss and Jansa (2009: 134–137), but including minor corrections and supplementary observations of character variation discovered in the course of this study.

creightoni), but absent in others (e.g., *M. pinheiroi*); maxillary fenestrae absent; posterolateral palatal foramina small, not extending anteriorly lingual to M4 protocones; posterior palate with prominent lateral corners (the choanae constricted behind). Maxillary and alisphenoid not in contact on floor of orbit (separated by palatine). Transverse canal foramen present. Alisphenoid tympanic process small, often bluntly conical or laterally compressed (never smoothly globular), always with a well-developed anteromedial process enclosing the extracranial course of mandibular nerve (secondary foramen ovale present), and not contacting rostral tympanic process of petrosal. Anterior limb of ectotympanic directly suspended from basicranium. Stapes triangular, with large obturator foramen. Fenestra cochleae exposed, not concealed by rostral and caudal tympanic processes of petrosal. Paroccipital process small, rounded, and adnate to petrosal. Dorsal margin of foramen magnum bordered by supraoccipital and exoccipitals, incisura occipitalis present.

Two mental foramina usually present on lateral surface of each hemimandible; angular process acute and strongly inflected.

Unworn crowns of I2–I5 symmetrically rhomboidal ("premolariform"), with subequal anterior and posterior cutting edges, increasing in length (mesiodistal dimension) from I2 to I5. Upper canine (C1) alveolus in premaxillary-maxillary suture; C1 without accessory cusps in some species (e.g., *M. creightoni*), or with only posterior accessory cusp (e.g., *M. invictus*), or with both anterior and posterior accessory cusps (e.g., *M. parvidens*). First upper premolar (P1) smaller than posterior premolars but well formed and not vestigial; second and third upper premolars (P2 and P3) subequal in height; P3 with posterior cutting edge only; upper milk premolar (dP3) large and molariform. Molars strongly carnassialized (postmetacristae much longer than postprotocristae); relative widths usually M1 < M2 < M3 < M4; centrocrista strongly inflected labially on M1–M3; ectoflexus shallow or indistinct on M1, shallow but usually distinct on M2, and consistently deep on M3; anterolabial cingulum and preprotocrista discontinuous (anterior cingulum incomplete) on M3 in some species (e.g., *M. noctivagus*), but anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete) in others (e.g., *M. parvidens*); postprotocrista without carnassial notch. Last upper tooth to erupt is P3.

Lower incisors (i1–i4) with distinct lingual cusps. Lower canine (c1) distinctively tall, recurved, and unicuspid in some species (e.g., *M. noctivagus*), but smaller and premolariform in others (e.g., *M. pinheiroi*). Second lower premolar (p2) subequal in height to p3 in some species (e.g., *M. incanus*) but distinctly taller than p3 in most others; lower milk premolar (dp3) trigonid complete. Hypoconid labially salient on m3; hypoconulid twinned with entoconid on m1–m3; entoconid usually taller than hypoconulid on m1–m3.

Remarks: As discussed by Voss and Jansa (2009: 137–138), the monophyly of the genus *Marmosops* is strongly supported by phylogenetic analyses of nuclear exon sequences and by combined analyses of nuclear genes and morphological characters. In the latter analyses, several morphological traits optimized as generic synapomorphies, including (1) spirally arranged caudal scales, (2) the petiolate morphology of the central hair in each caudal-scale triplet, and (3) the presence of a distinct rostral process of the premaxillae. Generic monophyly is also supported by unique deletions at the DMP1 and BRCA1 loci (Voss and Jansa, 2009: figs. 29, 31). The monophyly of *Marmosops* was additionally corroborated in recent phylogenetic analyses with much denser taxon sampling by Díaz-Nieto et al. (2016a, 2016b), who sequenced several genes not included in Voss and Jansa's (2009) study. As discussed elsewhere (Voss and Jansa, 2003: 56–57), DNA-DNA hybridization results reported by Kirsch and Palma (1995) and Kirsch et al. (1997) that recovered *Gracilinanus* nested inside the genus *Marmosops* are unambiguously attributable to misidentified voucher material. Diagnostic morphological comparisons among

Marmosops and other didelphid genera with which it was formerly confused (*Gracilinanus*, *Marmosa*, and *Thylamys*) were described, illustrated, and tabulated by Voss et al. (2004).

Subgenus *Sciophanes* Díaz-Nieto et al., 2016

Type species: *Marmosops parvidens* (Tate, 1931) by original designation.

Contents: Twelve species as described below.

Description: Combined length of head and body usually <120 mm and adult weight usually <30 g (except in *Marmosops carri* and *M. fuscatus*, both of which are substantially larger). Gular gland absent in all examined material. Lateral carpal tubercles consistently present in mature adult males; forearm with two widely separated antebrachial vibrissae. Mammae 3–1–3 = 7 or 4–1–4 = 9, all abdominal-inguinal (but note that mammary morphology is unknown for *M. fuscatus, M. juninensis, M. ojastii*, *M. pakaraimae*, and *M. magdalenae*). Scrotal integument consistently unpigmented and covered with self-whitish fur.

Nasals laterally expanded at or near maxillary-frontal suture (except in *M. carri* and *M. fuscatus*, which have very narrow, almost parallel-sided nasals). Interorbital region with rounded or squared supraorbital margins, without distinct beading and without distinct postorbital processes. Fenestra in parietal-squamosal suture consistently present; subsquamosal foramen anteroposteriorly elongate, exposing lateral surface of petrosal pars canalicularis behind sulcus for prootic sinus. Incisive foramina short, extending posteriorly between but not behind C1.

Upper canine (C1) with accessory cusps in one or both sexes (males of *Marmosops carri* and *M. fuscatus* lack C1 accessory cusps). Upper third molar (M3) with or without complete anterior cingulum (anterolabial cingulum and preprotocrista discontinuous in some species). Lower canine (c1) premolariform (procumbent, subequal in height to p1, and provided with a posterior accessory cusp) in most species (but not in males of *M. carri* and *M. fuscatus*, which have taller c1s that lack accessory cusps). Lower first molar (m1) entoconid and adjacent lower second molar (m2) paraconid subequal in height in some species, but m1 entoconid shorter than m2 paraconid in others.

Comparisons with the nominotypical subgenus: As explained by Díaz-Nieto et al. (2016a), species of *Sciophanes* can be unambiguously distinguished from species in the subgenus *Marmosops* by the morphology of the subsquamosal foramen (anteroposteriorly elongate in *Sciophanes*, anteroposteriorly constricted in *Marmosops*; fig. 9), C1 accessory cusps (present in one or both sexes in *Sciophanes*, consistently absent in *Marmosops*), and number of antebrachial vibrissae (two in *Sciophanes*, one in most *Marmosops*). However, the two subgenera also differ in their modal expression of other characters. In particular, most species of *Sciophanes* are small (HBL usually <120 mm, weight usually <30 g), whereas most members of the nominotypical subgenera are substantially larger. There is some size overlap, however, because two species of *Sciophanes* (*M. carri* and *M. fuscatus*; see below) are large, and because some species in the nominotypical subgenus (e.g., *M. ocellatus*; see Voss et al., 2004) are smaller than the subgeneric average. Nevertheless, wherever the two subgenera occur together (along the Rio Juruá, for example; Patton et al., 2000), species of *Sciophanes* are always smaller than sympatric members of the nominotypical subgenus.

Another potentially useful character for subgeneric identification is the morphology of the lower canine (c1), which is small (subequal in height to p1) and premolariform (with a well-developed posterior accessory cusp) in both sexes of most species of *Sciophanes*. By contrast, c1 is a larger tooth (always distinctly taller than p1) and often lacks a distinct posterior accessory cusp in members of the nominotypical subgenus. The noteworthy exceptions in this context are male specimens of the largest species of *Sciophanes* (*M. carri* and *M. fuscatus*), in which c1 is taller than p1 and lacks a distinct posterior accessory cusp.

Among external traits that are sometimes observed in the nominotypical subgenus, no spe-

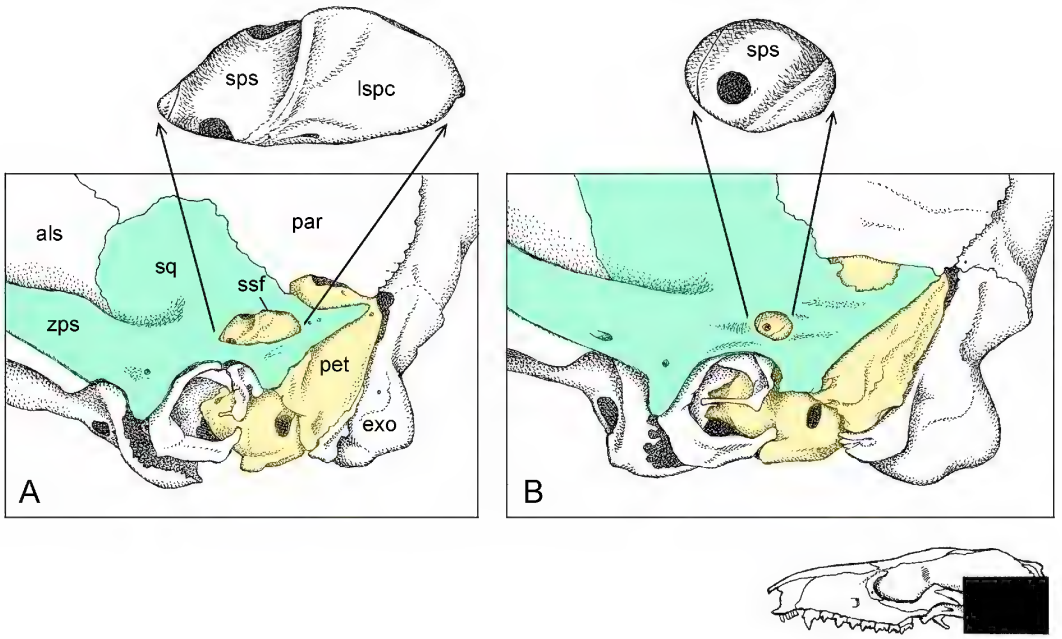

FIG. 9. Lateral view of posterior braincase of *Marmosops (Sciophanes) pinheiroi* (**A,** AMNH 267345) and *M. (M.) noctivagus* (**B,** MUSM 13288) illustrating diagnostic subgeneric morphologies of the squamosal (green) and petrosal (yellow). Abbreviations: **als,** alisphenoid; **exo,** exoccipital; **lspc,** lateral surface of *pars canalicularis* (of petrosal); **par,** parietal; **pet,** petrosal; **sps,** sulcus for the prootic sinus (of petrosal); **sq,** squamosal; **ssf,** subsquamosal foramen; **zps,** zygomatic process of the squamosal.

cies of *Sciophanes* has a gular gland, and none has dark-furred hind feet, "pectoral" mammae, or pigmented scrotal epithelium. Additionally, no species of *Sciophanes* has distinctly beaded supraorbital margins, develops postorbital processes, has long incisive foramina (extending behind the upper canines), or lacks a fenestra in the squamosal-parietal suture.

Remarks: The monophyly of *Sciophanes* is strongly supported by taxon-dense phylogenetic analyses of both nuclear and mitochondrial genes (Díaz-Nieto et al., 2016a, 2016b). Unfortunately, taxon-dense phylogenetic analyses incorporating morphological characters have yet to be completed, so it is not known which (if any) of the diagnostic external and craniodental traits described above might optimize as subgeneric synapomorphies.

The same molecular analyses that provided strong support for the monophyly of *Sciophanes* also recovered three well-supported species groups within this subgenus. Díaz-Nieto et al. (2016a: fig. 5) referred to these groups using alphabetical labels, for which we substitute other names in this report: the Fuscatus Group (for "clade A," including *Marmosops carri*, *M. fuscatus*, *M. handleyi*, and *M. invictus*), the Bishopi Group (for "clade B," including *M. bishopi*, *M. juninensis*, *M. ojastii*, and two new species), and the Parvidens Group (for "clade C," including *M. pakaraimae*, *M. parvidens*, and *M. pinheiroi*). All three groups are morphologically diagnosable (table 1).

Species of the Parvidens Group

Species of the Parvidens Group are distinguished from other members of the subgenus *Sciophanes* by their very long tails (averaging about 150% of HBL), spoon-shaped lateral carpal tubercles in adult males, consistent lack of palatine fenestrae, C1 with anterior and posterior

TABLE 1

Diagnostic Comparisons Among Species Groups of *Marmosops* (*Sciophanes*)

	Parvidens Group	Fuscatus Group	Bishopi Group
Geographic distribution	cis-Andean	Andean & trans-Andean	widespread
Ventral pelage	variable[a]	entirely gray-based	variable[a]
Relative tail length[b]	ca. 150%	<130%	<140%
Lateral carpal tubercles	spoon shaped	bladelike	bladelike
Mammae	3–1–3 or 4–1–4[c]	3–1–3[d]	4–1–4[e]
Palatine fenestrae	absent	variable[a]	variable[a]
C1 accessory cusps	present in both sexes[c]	variable[a]	variable[a]
M3 anterior cingulum	variable[a]	variable[a]	narrowly present
m1 entoconid & m2 paraconid	entoconid shorter	usually subequal	entoconid shorter

[a] Varies among member species.
[b] Length of tail divided by length of head-and-body, expressed as a percentage.
[c] Females of *Marmosops pakaraimae* are unknown.
[d] This character could not be scored for *Marmosops fuscatus*.
[e] This character could not be scored for *Marmosops juninensis*, *M. magdalenae*, or *M. ojastii*.

accessory cusps in both sexes, and c1 subequal in height to p1 (table 1). The three recognized species are all cis-Andean: restricted to the Guianas, eastern Venezuela, and eastern Amazonian Brazil (fig. 10). The following accounts are only slightly modified from those in Voss et al. (2013) and are based on substantially the same material that we examined in that earlier study. Diagnostic quantitative and qualitative comparisons are summarized in tables 2–4.

Marmosops pakaraimae Voss et al., 2013

Figures 11–13

Marmosops pakaraimae Voss et al., 2013: 6 (original description).

TYPE MATERIAL: The holotype (by original designation) consists of the skin, skull, postcranial skeleton, and preserved tissues of an adult male (ROM 115129; original number F46739) collected by Burton K. Lim and Deirdre M. Jafferally on 26 February 2003 at "Second Camp" on Mount Roraima (fig. 10: locality 49), Cuyuni-Mazaruni Region, Guyana. The other seven specimens listed below are all paratypes.

DISTRIBUTION, HABITATS, AND SYMPATRY: *Marmosops pakaraimae* is currently known from just five localities, of which three are in the Pakaraima Highlands of western Guyana and two are in the adjacent highlands of eastern Venezuela. Recorded elevations at these localities range from 800 m to about 1500 m above sea level, and recorded habitats are premontane or lower montane rain forest (Voss et al., 2013). This species is not definitely known to occur sympatrically with any congeneric species, although it might be expected to come into contact with *M. parvidens* and/or *M. pinheiroi* at lower elevations in western Guyana or eastern Venezuela.

DESCRIPTION: Body pelage dark brown (near Dark Umber) middorsally, but indistinctly paler laterally, and about 8–9 mm long at midback; ventral pelage superficially whitish (the ventral coloration contrasting abruptly with the brownish flanks), but hairs of throat, chest, abdomen, and inner surfaces of fore- and hind limbs uniformly gray based (only the apex of the chin, the oral margins, and the scrotum have self-white fur). Manus covered dorsally with uniformly pale hairs in some specimens (e.g., ROM 114698), but metacarpals distinctly darker than digits in others (ROM 115129); lateral carpal tubercles spoon shaped in all examined adult males. Mammary formula unknown (no female specimens examined). Tail much longer than combined length of head and body

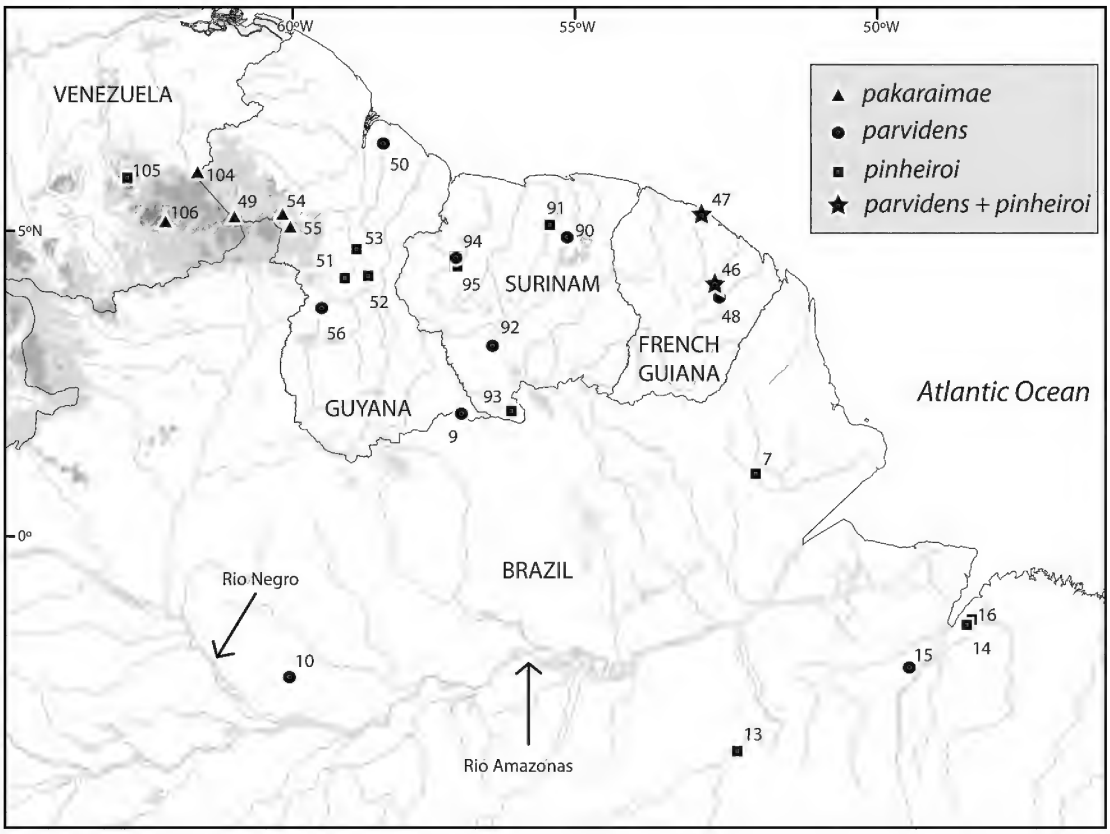

FIG. 10. Collecting localities of examined specimens of the Parvidens Group of *Sciophanes*. Numbers are keyed to entries in the gazetteer (appendix 1). Progressively darker shading indicates higher elevations: pale gray ≥500 m, medium gray ≥1000 m, dark gray ≥2000 m, darkest gray ≥3000 m.

(mean LT/HBL × 100 = 148%); dorsal caudal surface uniformly dark from base to tip, but ventral surface indistinctly paler (especially near the base of the tail).

Nasal bones long (consistently extending well behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae absent. Dorsolateral margin of ethmoid foramen formed by the orbitosphenoid.

Upper canine (C1) short, with anterior and posterior accessory cusps in males (female specimens are unknown). Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent. Entoconid of m1 apparently subequal to adjacent m2 paraconid;[3] unworn m4 talonid with three distinct cusps.

Comparisons: *Marmosops pakaraimae* averages larger than *M. parvidens* in most measured external dimensions (table 2), and the two species differ strikingly in dorsal pelage coloration (dark brown in *pakaraimae* versus paler and distinctly reddish brown in *M. parvidens*; Voss et al., 2013: fig. 2). The difference in ventral pel-

[3] This character is difficult to evaluate because specimens with unworn molars (juveniles and subadults) are unavailable.

TABLE 2

Measurements (mm) and Weights (g) of Adult Male Specimens of the Parvidens Group of *Marmosops* (*Sciophanes*)

	M. pakaraimae[a]	*M. parvidens*[b]	*M. pinheiroi*[c]
HBL	109 (104–116) 7	100 (93–107) 10	101 (85–121) 12
LT	161 (151–169) 7	150 (142–160) 10	150 (142–160) 12
HF	18 (17–19) 7	16 (15–17) 10	17 (16–18) 12
Ear	22 (22–23) 7	22 (21–24) 9	22 (20–25) 12
CBL	30.8 (29.8–31.9) 7	28.3 (27.3–29.1) 9	29.1 (28.4–29.8) 12
NL	14.6 (14.2–15.2) 4	13.7 (12.7–14.4) 9	14.1 (13.2–14.7) 11
NB	3.8 (3.5–4.0) 7	3.4 (2.9–3.6) 12	3.7 (3.1–4.2) 12
LIB	6.0 (5.8–6.2) 7	5.3 (4.9–5.5) 11	5.4 (5.2–5.7) 12
LPB	6.2 (6.0–6.6) 7	5.5 (5.2–5.7) 11	5.6 (5.2–5.9) 11
ZB	15.2 (14.8–15.7) 7	14.5 (13.9–15.0) 10	15.1 (14.6–16.0) 12
PL	17.3 (16.5–17.9) 7	16.0 (15.0–16.8) 10	16.3 (16.0–16.7) 11
PB	8.9 (8.2–9.4) 7	8.3 (8.0–8.7) 12	8.6 (8.2–8.9) 12
MTR	12.2 (11.9–12.6) 7	11.2 (11.0–11.6) 11	11.6 (11.3–12.0) 12
LM	6.1 (6.0–6.3) 7	5.5 (5.3–5.7) 12	5.7 (5.6–5.9) 12
M1–3	5.2 (5.2–5.4) 7	4.8 (4.6–5.2) 12	5.0 (4.8–5.2) 12
WM3	2.0 (2.0–2.1) 7	1.9 (1.8–2.0) 12	1.9 (1.8–2.0) 12
Weight	30 (25–33) 6	25 (21–31) 9	27 (22–33) 12

[a] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the type series (ROM 114698, 115129, 115148, 115254, 115841, 115845; USNM 385046).

[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 93970, 267347, 267348, 267353, 267359, 267361; MNHN 1995-929, 1995-930, 1995-933; ROM 114144, 117348; USNM 579989.

[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 266423, 267341, 267342, 267345, 267346, 267349, 267352, 267357; CM 63506; FMNH 95320; MNHN 1995-931, 1995-932; ROM 108920, 111558, 111663; USNM 461459, 461460, 461462–461465.

age coloration (op. cit.: fig. 3) is even more striking: whereas *M. pakaraimae* has almost completely gray-based ventral fur, all examined specimens of *M. parvidens* have a continuous streak of self-whitish fur that extends from chin to groin. *Marmosops pakaraimae* is consistently larger than *parvidens* in all measured craniodental dimensions, especially in five variables (CBL, LIB, LPB, MTR, LM) that exhibit nonoverlapping variation between our male samples (no female specimens of *M. pakaraimae* are known). Side-by-side comparisons of representative skulls (figs. 11–13) reveal that *M. pakaraimae* has a visibly broader interorbital region but relatively smaller orbits than *M. parvidens*. In qualitative aspects of craniodental morphology, however, these species are notably similar, both having lacrimal foramina that are mostly concealed from lateral view inside the anterior orbital margin, upper third molars with narrowly complete anterior cingula, and consistently tricuspid m4 talonids.

Marmosops pakaraimae also averages larger than *M. pinheiroi* in most external dimensions, and the two species differ in dorsal pelage color (dark brown in *M. pakaraimae* versus paler brownish gray in *M. pinheiroi*). The ventral fur of *M. pakaraimae* is also more extensively gray based than the ventral fur of *M. pinheiroi*, which usually includes a narrow, discontinuous midventral streak of self-white hairs. *Marmosops pakaraimae* is also larger on average than *M. pinheiroi* in craniodental mea-

TABLE 3

Measurements (mm) and Weights (g) of Adult Female Specimens of the Parvidens Group of *Marmosops* (*Sciophanes*)[a]

	M. parvidens[b]	*M. pinheiroi*[c]
HBL	96 (94–97) 2	100 (95–108) 15
LT	136 (133–138) 2	141 (125–154) 15
HF	16 (15–17) 2	16 (14–17) 15
Ear	21 (20–21) 2	20 (18–23) 15
CBL	27.3 (26.7–28.0) 4	28.5 (27.9–29.8) 14
NL	12.9 (12.7–13.4) 4	13.9 (13.4–14.6) 9
NB	3.1 (2.8–3.5) 5	3.3 (2.9–3.8) 14
LIB	5.2 (4.9–5.4) 4	5.4 (5.2–5.5) 15
ZB	14.5 (13.9–14.8) 5	15.1 (14.6–15.9) 12
PL	15.3 (14.9–15.8) 4	16.0 (15.5–16.8) 9
PB	8.3 (8.1–8.7) 5	8.8 (8.4–9.3) 14
MTR	11.1 (11.1–11.2) 5	11.6 (11.2–12.1) 15
LM	5.5 (5.3–5.6) 5	5.8 (5.5–6.2) 15
M1–3	4.8 (4.7–4.9) 5	5.0 (4.8–5.4) 15
WM3	1.9 (1.9–2.0) 5	2.0 (1.8–2.1) 15
Weight	22	22 (19–25) 11

[a] Female specimens of *Marmosops pakaraimae* are unknown.
[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 97333, 267344; FMNH 18545; USNM 548439, 579990.
[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 130570, 267342 267352; CM 63506; FMNH 95320; USNM 393529–393532, 461459, 461460, 461462, 461464, 461465, 545543.

surements, especially in three dimensions (LIB, LPB, and LM) that exhibit nonoverlapping variation in our samples. Visual comparisons of representative skulls (figs. 11–13) reveal similar proportional differences between *M. pakaraimae* and *M. pinheiroi* to those previously noted between *M. pakaraimae* and *M. parvidens*, namely that *M. pakaraimae* has a relatively broader interorbit but smaller orbits. Additionally, the lacrimal foramina are more prominently exposed laterally, M3 never has a complete anterior cingulum, and m4 often has a bicuspid talonid in *M. pinheiroi.*

Specimens examined (N = 8): **Guyana**—*Cuyuni-Mazaruni,* Mt. Roraima (ROM 115129, 115148, 115254); *Potaro-Siparuni,* Mt. Ayanganna (ROM 114698), Mt. Wokomung (ROM 115841, 115845). **Venezuela**—*Bolívar,* 85 km SSE El Dorado (USNM 385046), Churi-tepui (AMNH 176353).

Marmosops parvidens (Tate, 1931)

Figures 2, 5A, 7A, 11–13, 14A

Marmosa parvidens Tate, 1931: 13 (original description).

Marmosa parvidens parvidens: Pine, 1981: 60 (name combination).

Marmosops parvidens: Gardner and Creighton, 1989: 4 (name combination).

Type material: The holotype (by original designation) consists of the skin and skull of an adult female (FMNH 18545; original number 8) collected by S.B. Warren on 8 September 1906 at Hyde Park (fig. 10: locality 50), a locality near sea level on the Demerara River in East Demerara–West Coast Berbice about 35 km south of Georgetown. No other specimens were mentioned in the original description of this species.

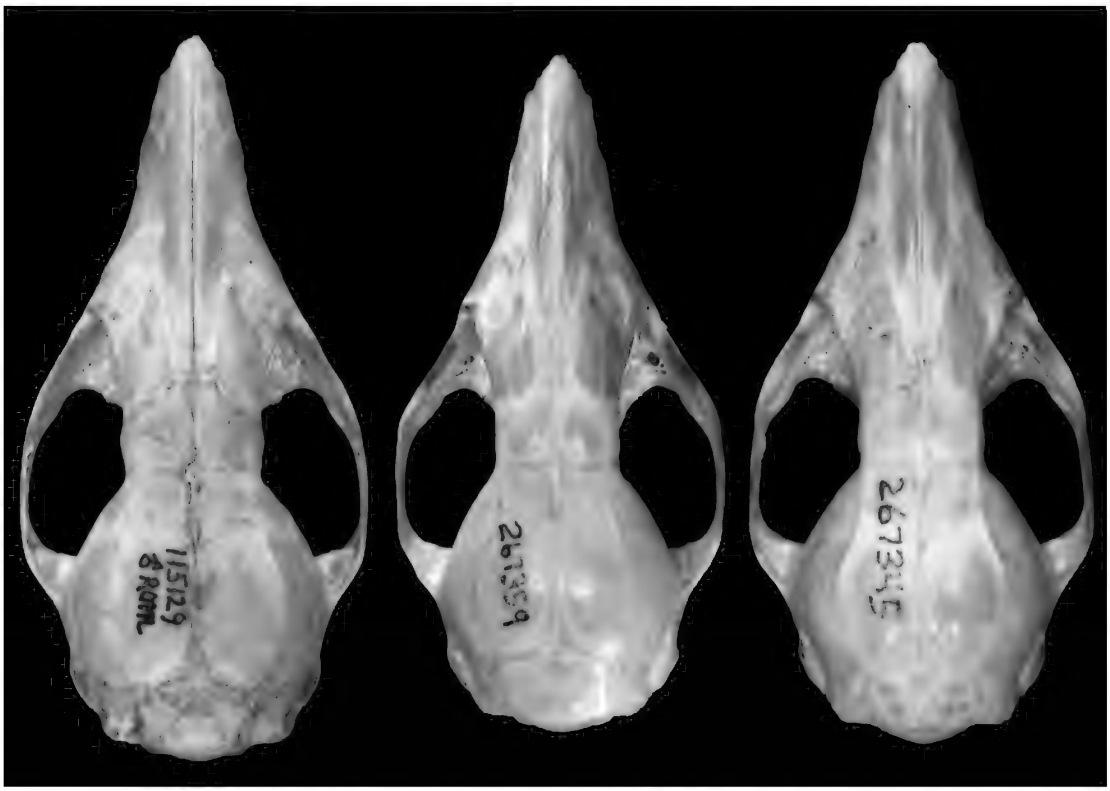

FIG. 11. Dorsal views of skulls of the Parvidens Group of *Sciophanes*. Left to right: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (AMNH 267359), and *M. pinheiroi* (AMNH 267345). All views about ×3.

Distribution, habitats, and sympatry: Examined specimens suggest that *Marmosops parvidens* occurs throughout most of the Guiana Region (north of the Amazon and east of the Rio Negro), but the species appears to be unknown from Venezuela (García et al., 2014), and we have not examined any material from northern Pará. Although we have not personally examined material from Amapá, *M. parvidens* has recently been reported to occur there (Silva et al., 2013). A single specimen is also known from SE Amazonia (on the lower Rio Tocantins, fig. 10: locality 13). All specimens associated with definite elevational data were collected between sea level and about 500 m. The predominant vegetation throughout the range of this species, which broadly overlaps that of *M. pinheiroi*, is lowland rain forest (e.g., in French Guiana, where both species occur sympatrically; Voss et al., 2001; Catzeflis et al., 2014).

Description: Body pelage dusty reddish brown (near Bister or Snuff Brown) middorsally, but indistinctly paler laterally, and about 6–8 mm long at midback; ventral pelage extensively self-white from chin to anus (including the inner surfaces of the fore- and hind limbs), usually with only narrow lateral-abdominal borders of gray-based fur. Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercles spoon shaped in all examined adult males. Mammae 3–1–3 = 7 or 4–1–4 = 9. Tail much longer than combined length of head and body (mean LT/HBL × 100 = 150%); dorsal caudal surface uniformly dark from base to tip, but ventral surface indistinctly paler (especially near the base of the tail).

Nasal bones long (extending well behind the lacrimals) and much wider posteriorly than ante-

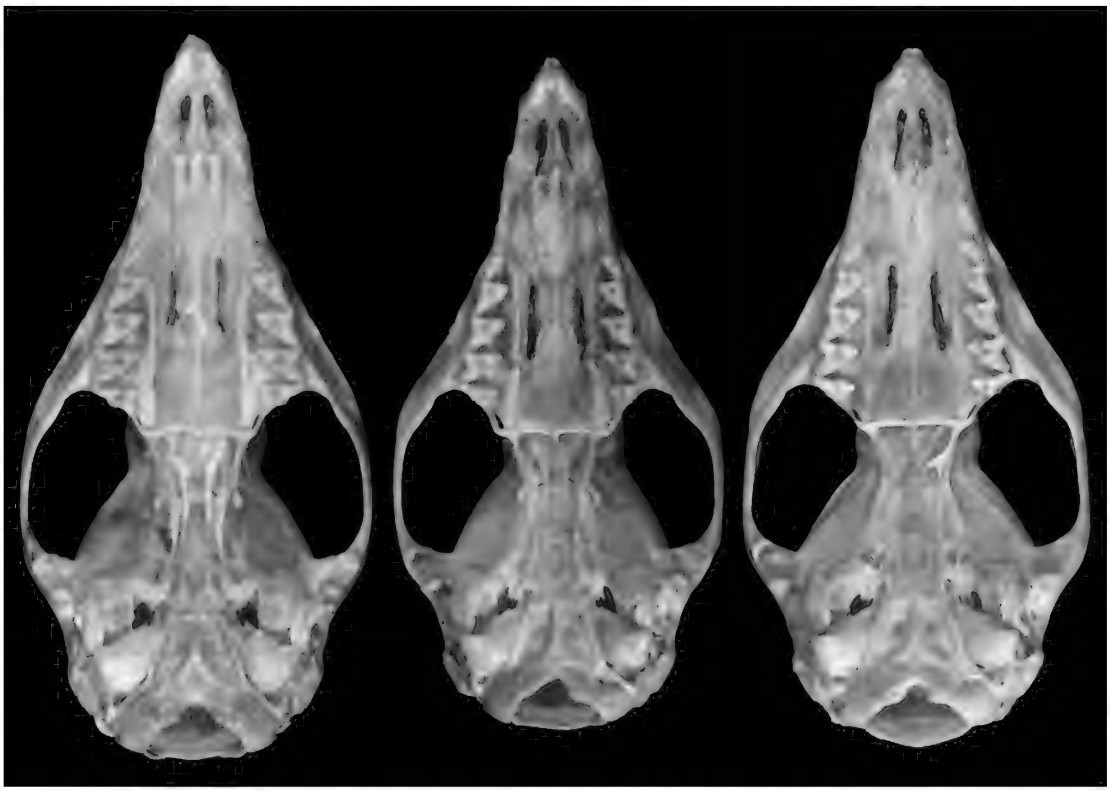

FIG. 12. Ventral views of skulls of the Parvidens Group of *Sciophanes*. Left to right: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (AMNH 267359), and *M. pinheiroi* (AMNH 267345). All views about ×3.

riorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina usually concealed from lateral view inside anterior orbital margin; zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae absent. Dorsolateral margin of ethmoid foramen usually formed by the orbitosphenoid.

Upper canine (C1) short, with anterior and posterior accessory cusps in both sexes. Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent. Entoconid of m1 subequal in height to adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

Comparisons: *Marmosops parvidens* is approximately the same size as *M. pinheiroi* (tables 2, 3) in external dimensions, and differences in dorsal pelage coloration (usually some shade of dusty reddish brown in *M. parvidens* versus dull brownish gray in *M. pinheiroi*) are sometimes less than obvious. By contrast, ventral pelage coloration provides a consistently useful external criterion for separating these broadly sympatric species: whereas *M. parvidens* has a broad, continuous band of self-whitish fur that extends from chin to groin and along the inner surfaces of the fore- and hind limbs, *M. pinheiroi* has a much narrower, discontinuous midventral streak of self-white hairs that apparently never extends onto the throat nor along the inner surfaces of the fore- and hind limbs. *Marmosops parvidens* averages smaller than *pinheiroi* in most craniodental dimensions (WM3 in males is the unique exception; tables 2, 3), but all measurements show overlapping variation between the

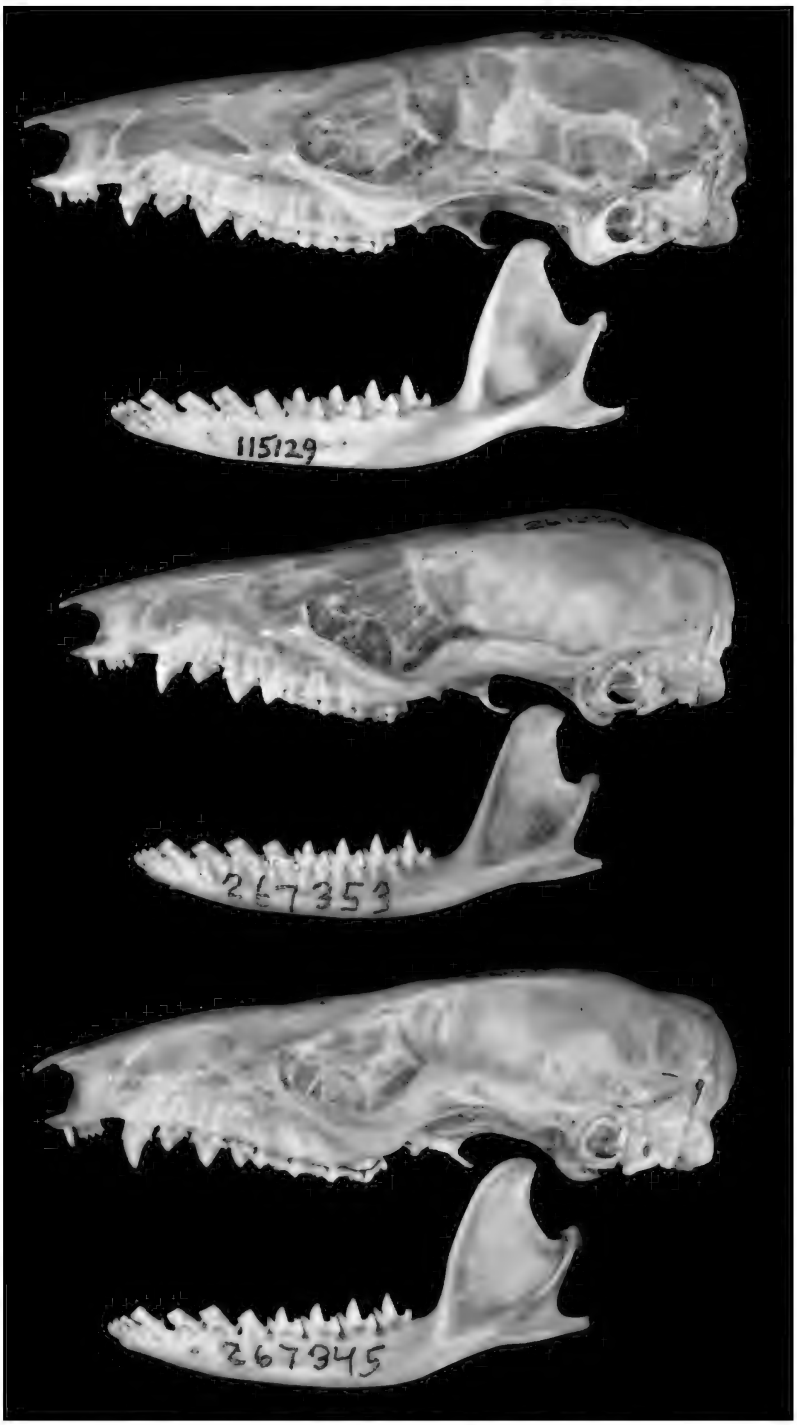

FIG. 13. Lateral views of skulls and mandibles of the Parvidens Group of *Sciophanes*. Top to bottom: *Marmosops pakaraimae* (ROM 115129, holotype), *M. parvidens* (AMNH 267359 [skull], 267353 [mandible]), and *M. pinheiroi* (AMNH 267345). All views about ×3.

TABLE 4

Diagnostic Morphological Comparisons among Members of the Parvidens Group of *Marmosops* (*Sciophanes*)

Character	*M. pakaraimae*	*M. parvidens*	*M. pinheiroi*
Dorsal pelage	dark brown	paler, usually reddish brown	paler, usually grayish brown
Ventral pelage	gray-based	mostly self-whitish	mostly gray-based, but variable
Lacrimal foramina	concealed inside orbit	concealed inside orbit	laterally exposed anterior to orbit
M3 anterior cingulum	narrowly complete	narrowly complete	incomplete
m4 talonid	tricuspid	tricuspid	often bicuspid

two species, so none is diagnostic (despite unambiguous multivariate separation; Voss et al., 2001: fig. 24). Instead, qualitative aspects of craniodental morphology provide better characters for species identification: (1) whereas *M. parvidens* has lacrimal foramina that are usually concealed within the orbit (fig. 14A), the lacrimal foramina of *M. pinheiroi* are more prominently exposed laterally (fig. 14B); (2) the dorsolateral margin of the ethmoid foramen is usually formed by the orbitosphenoid in *M. parvidens*, whereas the corresponding bony margin in *M. pinheiroi* is often formed by the frontal; (3) the unworn M3 of *M. parvidens* has a narrowly complete anterior cingulum, whereas the anterolabial cingulum and preprotocrista of this tooth are discontinuous in *M. pinheiroi*; (4) the talonid of m4 is consistently tricuspid in *M. parvidens* but often appears to be bicuspid in *M. pinheiroi*.

Comparisons between *Marmosops parvidens* and *M. pakaraimae* are provided in the account of the latter species (above).

Remarks: The binomina "*Marmosa parvidens*" and "*Marmosops parvidens*" were previously applied to specimens of several distinct species, including *M. bishopi*, *M. juninensis*, *M. ojastii*, *M. pakaraimae*, and others (e.g., by Handley, 1976; Pine, 1981; Linares, 1998; Patton et al., 2000). The restricted sense in which this species is now understood was first defined by Voss et al. (2001). Current phylogeographic sampling of *M. parvidens* consists of 10 cytochrome-*b* sequences from six localities in French Guiana, Guyana, and Surinam; these differ from one another by an average uncorrected distance of just 1.6%, well below the threshold value for species recognition in coalescent analyses performed by Díaz-Nieto et al. (2016a). Additionally, we have not observed any geographic variation in morphology that corresponds to geographic variation in cytochrome-*b* sequence data from this species.

We carefully reexamined AMNH 97333, which remains the only specimen of *Marmosops parvidens* collected south of the Amazon. Although this specimen differs from material collected north of the Amazon in having the dorsolateral margin of the ethmoid foramen bordered by the frontal, and by lacking a continuous anterior cingulum on M3, it closely resembles typical *M. parvidens* in other respects, notably in its extensively self-white ventral pelage. Although molecular confirmation that *M. parvidens* occurs south of the Amazon would be welcome, we feel reasonably confident in the current identification of this unique specimen.

Specimens examined (N = 42): **Brazil**—*Amazonas,* Boca Rio Paratucu (AMNH 93970), 80 km N Manaus (INPA 1758, 1762–1769, 1772–1779; USNM 579985–579989); *Pará,* Ilha do Taiuna (AMNH 97333). **French Guiana**—Les Nouragues (ISEM V-1633), Paracou (AMNH 267344, 267347, 267348, 267353, 267359, 267361; MNHN 1995-929, 1995-933, 1995-939), River Arataye (USNM 548439). **Guyana**—*Demerara-Mahaica,* Hyde Park (FMNH 18545), *Upper Takutu–Upper Essequibo,* Karanambo (ROM 97938). **Surinam**—*Brokopondo,* Brownsberg Nature Park (ROM 113997, 114009, 114144); *Nickerie,* Kayser Gebergte Airstrip (FMNH 93169); *Sipaliwini,* Bakhuis Transect 13 (ROM 117348).

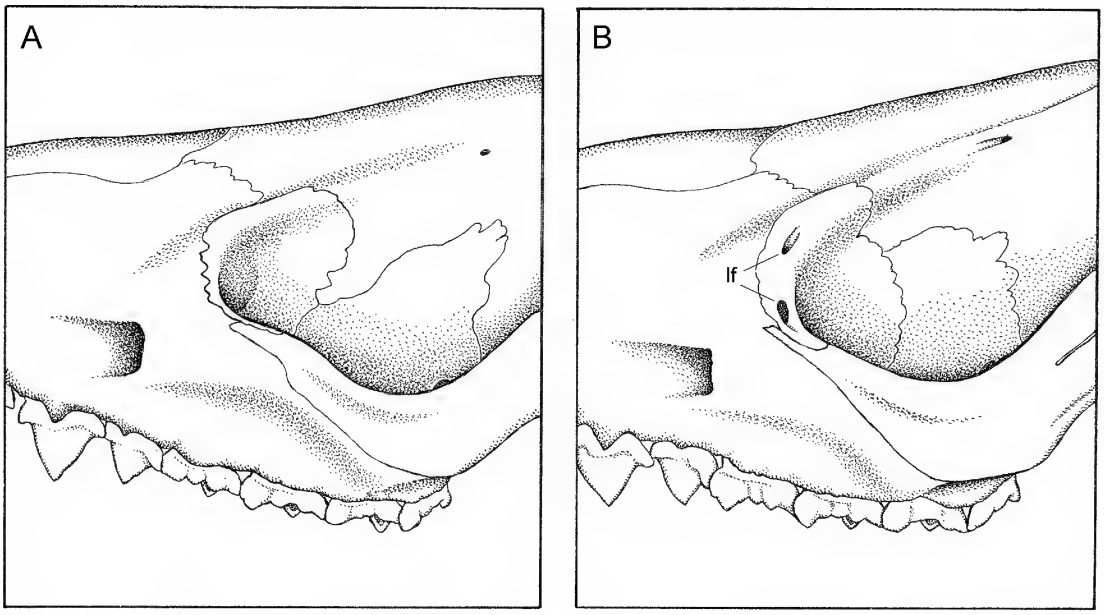

FIG. 14. Lateral views of the anterior orbital region of *Marmosops parvidens* (**A,** AMNH 267359) and *M. pinheiroi* (**B,** AMNH 267345) illustrating species differences in the lacrimal foramina (**lf**), which are usually concealed inside the orbit in *M. parvidens*, but which are laterally exposed on the orbital margin of *M. pinheiroi*.

Marmosops pinheiroi (Pine, 1981)

Figures 1, 3A, 6A, 9A, 11–13, 14B

Marmosa parvidens pinheiroi Pine, 1981: 61 (original description).

Marmosa parvidens woodalli Pine, 1981: 62 (original description). Type locality "Nova Area Experimental, Utinga (the wooded area surrounding the Belém waterworks), Belém (1°27′ S, 48°29′ W), Pará, Brazil."

Marmosops parvidens: Gardner, 1993: 20, part (name combination; *pinheiroi* and *woodalli* listed as synonyms).

Marmosops pinheiroi: Voss et al., 2001: 49 (first use of current binomial).

Type material: The holotype (by original designation) consists of the skin and skull of an adult male (USNM 461459, original numbers T-391 and L5049), said to have been collected by personnel of the Instituto Evandro Chagas on 8 May 1969 at Rio Amapari, Serra do Navio (fig. 10: locality 7), Amapá, Brazil. In addition, Pine (1981) examined 15 other specimens (paratypes), but one of these (USNM 385045) is also a paratype of *M. pakaraimae*, and two others (AMNH 130521, USNM 385046) might also be referable to the latter species (Voss et al., 2013).

Distribution, habitats, and sympatry: Based on the material we examined, *Marmosops pinheiroi* occurs in eastern Venezuela, Guyana, Surinam, French Guiana, and Brazil (Amapá and eastern Pará). We have not examined the specimens that Nascimento et al. (2015) recently identified as *M. pinheiroi* from the Brazilian state of Maranhão, which would be a significant ecogeographic range extension if their material were correctly identified (see Remarks, below). Throughout its known range, this species probably cooccurs with *M. parvidens*, but the two have been collected sympatrically only in French Guiana (Voss et al., 2001; Catzeflis et al., 2014). Specimens of *M. pinheiroi* associated with definite elevational data were collected from near sea level to about 500 m. The predominant vegetation throughout the geographic range of this species—as documented by

examined specimens—is lowland rain forest (e.g., at Paracou, French Guiana; Voss et al., 2001).

Description: Body pelage brownish gray (near Olive Brown or Fuscous) middorsally, but indistinctly paler laterally, and about 6–8 mm long at midback; ventral pelage superficially whitish but extensively gray based in most specimens (only the chin, groin, and a narrow midventral streak of abdominal fur are usually self-white); inner surfaces of fore- and hind limbs covered with gray-based fur, apparently never self-white. Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercles spoon shaped in all examined adult males. Mammae 3–1–3 = 7 or 4–1–4 = 9. Tail much longer than combined length of head and body (mean LT/HBL × 100 = 150%); dorsal caudal surface uniformly dark from base to tip, but ventral surface indistinctly paler (especially near the base of the tail).

Nasal bones long (extending well behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina usually exposed in lateral view; zygomatic process of squamosal bone broadly overlapped dorsally by the jugal. Palatine fenestrae absent. Dorsolateral margin of ethmoid foramen formed by the orbitosphenoid in some specimens (e.g., ROM 108920, AMNH 267340, 267346), by the frontal in others (e.g., AMNH 267341, 267342), occasionally with bilateral variation (e.g., AMNH 267345).

Upper canine (C1) short, apparently always with anterior and posterior accessory cusps in both sexes. Upper third molar (M3) anterolabial cingulum discontinuous with preprotocrista (anterior cingulum incomplete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and subequal in height to p1; c1 anterolingual accessory cusp absent. Entoconid of m1 shorter than adjacent m2 paraconid in some specimens (e.g., AMNH 266423, 267342, 267345), but these cusps subequal in others (e.g., AMNH 267349, 267357); unworn m4 talonid often with only two distinct cusps.

Comparisons: Diagnostic comparisons of *Marmosops pinheiroi* with *M. pakaraimae* and *M. parvidens* are provided in earlier species accounts (see above).

Remarks: In our previous analyses of molecular sequence data (Voss et al., 2013; Díaz-Nieto et al., 2016a), we recovered two cytochrome-*b* haplogroups among the material here referred to *Marmosops pinheiroi*, the first consisting of six sequences from the Guianas and the second including two sequences from southeastern Pará (south of the Amazon and east of the Rio Xingu). On the assumption that these haplogroups are physically separated by the lower Amazon, then the epithet *pinheiroi* could be associated with the former group and *woodalli* with the latter. Although this phylogeographic structure is robustly supported, these haplogroups differ on average by only 3.9% in uncorrected pairwise sequence comparisons, and we are unable to morphologically distinguish their corresponding voucher material. Therefore, we continue to treat *woodalli* as a junior (subjective) synonym.

The specimens that Nascimento et al. (2015) identified as *Marmosops pinheiroi* extend the potential range of this species by almost 700 km, into the Brazilian state of Maranhão. These specimens are also remarkable for having been collected in savanna, whereas all others known to us have been taken in lowland rain forest. Unfortunately, the identification of this interesting material is apparently based only on sequence analysis and external measurements. Supporting evidence from craniodental morphology would be very welcome.

Specimens examined (N = 33): **Brazil**—*Amapá,* Serra do Navio (USNM 461459, 461460, 461462–461465); *Pará,* 52 km SSW Altamira (USNM 549294), Belém (USNM 545543), Utinga (USNM 393529–393532, 393534). **French Guiana**—Paracou (AMNH 266423, 267340, 267341, 267342, 267345, 267346, 267349, 267352, 267357; MNHN 1995-931, 1995-932). **Guyana**—*Potaro-Siparuni,* Forest Canopy Walkway (ROM 119852), 10 km NW Kurupukari (ROM 108920), Kabukalli Landing (ROM 111558, 111663). **Surinam**—*Bokopondo,*

TABLE 5
Measurements (mm) and Weights (g) of Adult Male Specimens of the Fuscatus Group of *Marmosops* (*Sciophanes*)

	M. carri[a]	*M. fuscatus*[b]	*M. handleyi*[c]	*M. invictus*[d]
HBL	139 (126–155) 17	136 (132–140) 2	116 (110–122) 2	111 (106–115) 5
LT	169 (152–183) 17	149 (147–150) 2	149 (149–149) 2	136 (124–147) 5
HF	21 (20–23) 17	20 (19–20) 2	19 (19–20) 2	18 (17–19) 5
Ear	26 (23–29) 17	25	21 (20–21) 2	21 (21–22) 3
CBL	36.7 (33.8–41.2) 20	33.3 (31.8–35.4) 5	29.1 (27.7–30.5) 2	30.0 (29.8–30.3) 4
NL	18.1 (15.6–20.4) 17	15.9 (15.2–16.7) 5	14.2 (12.7–15.6) 2	14.5 (14.1–14.9) 5
NB	3.1 (2.7–3.5) 22	3.1 (2.7–3.3) 5	3.6 (3.5–3.7) 2	3.5 (3.2–3.8) 5
LIB	6.5 (6.2–7.0) 20	6.3 (6.0–6.6) 5	5.8 (5.5–6.0) 2	5.9 (5.7–6.0) 5
ZB	19.5 (17.1–21.8) 20	17.7 (16.5–19.5) 4	15.0 (14.5–15.5) 2	15.8 (15.2–16.1) 4
PL	20.8 (19.1–23.0) 21	18.9 (18.4–19.6) 5	16.1 (15.3–17.0) 2	16.6 (16.2–17.0) 5
PB	10.9 (10.1–11.8) 22	10.0 (9.7–10.7) 5	8.5	9.0 (8.6–9.5) 5
MTR	15.2 (14.3–17.2) 22	13.6 (13.3–13.9) 5	12.0 (11.6–12.5) 2	12.3 (12.1–12.5) 5
LM	7.2 (7.0–7.7) 22	6.6 (6.5–6.7) 5	6.1 (6.0–6.3) 2	6.3 (6.3–6.5) 5
M1–3	6.2 (5.9–6.5) 22	5.7 (5.7–5.7) 5	5.3 (5.2–5.5) 2	5.4 (5.3–5.7) 5
WM3	2.3 (2.1–2.5) 22	2.2 (2.1–2.2) 5	1.7	2.1 (2.0–2.2) 5
Weight	60 (41–85) 10	69	30	—

[a] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 150007, 186437, 186438, 214439, 259978; KU 372934; USNM 370023, 370024, 370031, 370034, 370035, 370039, 372934, 406926, 406928, 406931, 418515, 443787, 443789, 517258–517260.
[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 276509, 276580; BMNH 3.1.5.2, 3.1.5.3; FMNH 22174.
[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: CTUA 433; FMNH 69823.
[d] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: USNM 178708, 309265, 309267, 337960, 337962.

Finisanti (FMNH 95320); *Nickerie,* Sipaliwini Airstrip (CM 63506); *Sipaliwini,* Bakhuis Transect (ROM 116974). **Venezuela**—*Bolívar,* Auyántepui (AMNH 130568, 130570).

Species of the Fuscatus Group

Species of the *Marmosops fuscatus* group are distinguished from other members of the subgenus *Sciophanes* by their entirely gray-based ventral fur, bladelike lateral carpal tubercles (in adult males), females with 3–1–3 = 7 mammae, and m1 entoconid usually subequal to the adjacent m2 paraconid. The four recognized species are found in eastern Panama, the northern part of the Cordillera Central of Colombia, the Cordillera de Mérida in western Venezuela, the coastal sierras and adjacent rain-forested lowlands of northern Venezuela, and the continental-shelf islands of Trinidad and Tobago. Diagnostic quantitative and qualitative comparisons are summarized in tables 5–7.

Marmosops carri (Allen and Chapman, 1897)

Figures 6C, 7B, 8B, 15, 16

Thylamys carri Allen and Chapman, 1897: 27 (original description).

Didelphys (*Marmosa*) *carri:* Trouessart, 1905: 856 (name combination).

Marmosa (*Thylamys*) *carri:* Cabrera, 1919: 40 (name combination).

Marmosops fuscatus: Gardner, 1993: 19; part (*carri* treated as a subjective junior synonym of *fuscatus* Thomas, 1896)

TABLE 6
Measurements (mm) and Weights (g) of Adult Female Specimens of the Fuscatus Group of *Marmosops* (*Sciophanes*)

	M. carri[a]	*M. fuscatus*[b]	*M. handleyi*[c]	*M. invictus*[d]
HBL	130 (125–134) 5	—	109 (104–113) 5	109 (104–112) 5
LT	156 (145–171) 5	—	135 (129–141) 5	133 (124–140) 5
HF	20 (19–21) 5	—	18 (17–19) 5	17 (17–18) 5
Ear	25 (24–26) 5	—	20 (19–21) 5	22 (21–22) 4
CBL	33.7 (32.3–34.9) 6	—	29.9 (29.4–30.7) 5	29.3 (28.2–29.9) 5
NL	16.1 (15.1–16.5) 6	—	15.1 (14.5–15.5) 5	14.1 (13.6–14.9) 5
NB	2.9 (2.5–3.2) 6	3.6	3.5 (3.3–3.7) 5	3.6 (3.3–4.1) 5
LIB	6.2 (6.0–6.4) 6	6.1	6.0 (5.9–6.2) 5	5.9 (5.7–6.1) 5
ZB	17.1 (16.1–17.7) 4	—	15.1 (14.5–15.5) 4	15.7 (14.9–16.2) 5
PL	19.3 (19.1–19.6) 5	18.0	16.7 (16.3–17.0) 5	16.5 (16.0–17.0) 5
PB	10.7 (10.3–11.3) 5	9.4	9.0 (8.8–9.4) 5	9.2 (9.1–9.5) 5
MTR	14.4 (13.9–15.0) 6	13.0	12.5 (12.0–12.9) 5	11.9 (11.8–12.1) 5
LM	7.2 (7.0–7.6) 6	6.3	6.3 (5.9–6.6) 5	6.2 (6.0–6.4) 5
M1–3	6.2 (5.9–6.5) 6	5.5	5.4 (5.2–5.6) 5	5.3 (5.2–5.5) 5
WM3	2.3 (2.2–2.6) 6	2.2	1.6	2.1 (2.0–2.1) 5
Weight	42 (41–42) 2	—	27 (21–31) 4	—

[a] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 5921; USNM 370030, 370037, 406929, 443786, 517256.
[b] Measurements of BMNH 96.11.1.6 (holotype).
[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: CTUA 411, 413, 414, 416; FMNH 69838.
[d] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: USNM 178709, 306386, 309266, 337959, 337961.

Marmosops fuscatus carri: Gardner and Creighton, 2008: 66 (name combination).

Marmosops fuscatus fuscatus: Gardner and Creighton, 2008: 66 (name combination); part (Venezuelan material of *carri* misidentified as *M. f. fuscatus*).

TYPE MATERIAL: The holotype (by original designation) consists of the skin and skull of an adult male (AMNH 7314/5922, original number 731) collected by Frank M. Chapman at Caparo (fig. 17: locality 97), Trinidad, on 20 March 1894. Two other specimens (paratypes) were also part of Allen and Chapman's type series: one is AMNH 7313/5921 (a young adult female), and the other was AMNH 7315/5923 (said to be an adult male; not examined and presumed lost).

DISTRIBUTION, HABITATS, AND SYMPATRY: *Marmosops carri* is known from Trinidad, Tobago, and Venezuela (fig. 17).[4] On the Venezuelan mainland, examined specimens have been collected in premontane and montane rain forest along the northern coastal cordilleras (e.g., at Hotel Humboldt; Handley, 1976: 79) and the Cordillera de Trujillo (e.g., at Hacienda Misisí; Handley, 1976: 71) between about 1000 m and 2300 m (but see Remarks). On Trinidad, however, it is definitely known to occur near sea level (e.g., at Rio Grande Forest; Appendix 1: locality 100), presumably in lowland rain forest. Although the known range of *M. carri* overlaps with that of *M. ojastii* (a member of the Bishopi Group; see below) and might be expected to contact that of *M. fuscatus*, these species have apparently not been collected sympatrically.

[4] Our material of *Marmosops carri* from Tobago, the first to be reported from that island, was originally identified as such by Darrin P. Lunde.

TABLE 7
Diagnostic Morphological Comparisons among Members of the Fuscatus Group of *Marmosops* (*Sciophanes*)

Character	*M. carri*	*M. fuscatus*	*M. handleyi*	*M. invictus*
Dorsal pelage of manus	all-white	all-white	metacarpals dark	metacarpals dark
Nasal shape	uniformly narrow	uniformly narrow	wider posteriorly	wider posteriorly
Palatine fenestrae	variable	variable	present	absent
C1 accessory cusps	♂: absent	♂: absent	♂: posterior only	♂: posterior only
	♀: variable	♀: posterior only	♀: anterior & posterior	♀: posterior only
Heights c1, p1 (males)	c1 > p1	c1 > p1	c1 ≈ p1	c1 ≈ p1
c1 lingual accessory cusp	absent	absent	present	usually present
m1 entoconid, m2 paraconid	subequal	subequal	subequal	m2 paraconid taller
Length of molars (LM)	7.0–7.7 mm	6.0–6.7 mm[a]	5.9–6.6 mm	6.0–6.5 mm

[a] Observed range includes measurements from two subadults (USNM 418503, 442719) with completely erupted molar dentitions (not included in tables 5 and 6).

DESCRIPTION: Body pelage grayish brown (near Fuscous or Hair Brown) middorsally, sometimes indistinctly paler laterally, and about 7–9 mm long at midback; ventral pelage superficially whitish, but hairs of throat, chest, and abdomen uniformly gray based in most specimens (a few have patches or narrow streaks of self-white fur on the throat, chest, groin, or along the insides of the thighs; e.g., AMNH 144832, USNM 370037). Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercles bladelike in all examined adult males. Mammae 3–1–3 = 7 in all examined females with visible teats. Tail longer than combined length of head and body (mean LT/HBL × 100 = 120%); dorsal caudal surface dark, but indistinctly paler distally in some specimens; ventral caudal surface distinctly paler than dorsal surface.

Nasal bones long (extending well behind the lacrimals) and uniformly narrow, without conspicuous lateral expansion at the maxillary-frontal suture. Interorbital region broad, with rounded supraorbital margins in females and young adult males, but relatively narrower and tending to develop squared supraorbital margins in large adult males; postorbital processes absent or indistinct. Lacrimal foramina usually visible in lateral view; zygomatic process of the squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae present or absent (when present, palatine fenestrae usually consist of several small irregular perforations, but in a few specimens they are large). Dorsolateral margin of ethmoid foramen usually formed by the orbitosphenoid.

Upper canine (C1) sexually dimorphic (taller and unicuspid in males, shorter and with one or two accessory cusps in females).[5] Upper third molar (M3) anterolabial cingulum discontinuous with preprotocrista (anterior cingulum incomplete). Lower canine (c1) sexually dimorphic (erect, without accessory cusps, and taller than p1 in males versus procumbent, with posterior accessory cusp, and subequal in height to p1 in females); c1 anterolingual accessory cusp usually absent in both sexes. Entoconid of m1 apparently subequal to m2 paraconid (but few specimens with unworn molars examined for this trait); unworn m4 talonid with three distinct cusps.

COMPARISONS: *Marmosops carri* is externally similar to *M. fuscatus* (with which it was formerly synonymized; see Remarks) but has somewhat paler dorsal fur, averages larger in all external measurements (tables 5, 6), and has a relatively longer tail (e.g., LT/HBL ×100 = 122%

[5] All examined females have posterior accessory C1 cusps, and insular populations (from Trinidad and Tobago) usually also have small anterior accessory cusps (e.g., AMNH 5921, 234951, 234954, 234956, 259979). By contrast, females from mainland populations usually lack anterior accessory cusps on C1 (e.g., AMNH 144832; USNM 370030, 517256).

FIG. 15. Dorsal and ventral views of skulls of *Marmosops carri* (left, AMNH 259978) and *M. fuscatus* (right, AMNH 276580). All views about ×2.5.

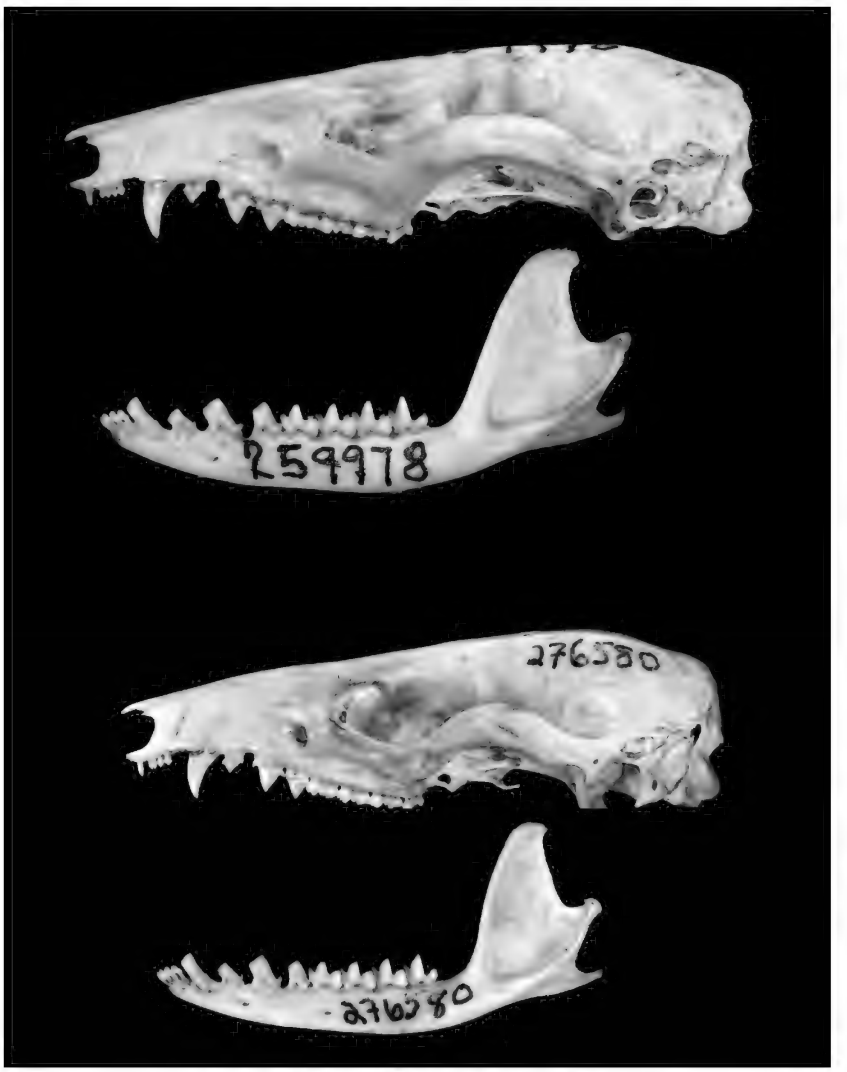

FIG. 16. Lateral views of skulls and mandibles of *Marmosops carri* (above, AMNH 259978) and *M. fuscatus* (below, AMNH 276580). All views about ×2.5.

in male *carri* versus 110% in male *fuscatus*). *Marmosops carri* averages larger than *M. fuscatus* in all measured craniodental dimensions (except nasal breadth, NB) but especially in three dental dimensions (MTR, LM, M1–3) that exhibit nonoverlapping variation. In other (qualitative) aspects of craniodental morphology the two species cannot be consistently distinguished, although there are modal differences in some characters. For example, the dorsolateral margin of the ethmoid foramen is usually formed by the orbitosphenoid in *M. carri*, whereas this foramen is bordered dorsolaterally by the frontal in *M. fuscatus*. Handley and Gordon (1979) implied that *carri* and *fuscatus* (which they regarded as no more than subspecifically distinct) differ in nasal morphology—the nasals were said to be more expanded posteriorly in *fuscatus* than in *carri*—but we did not observe a consistent taxonomic difference in

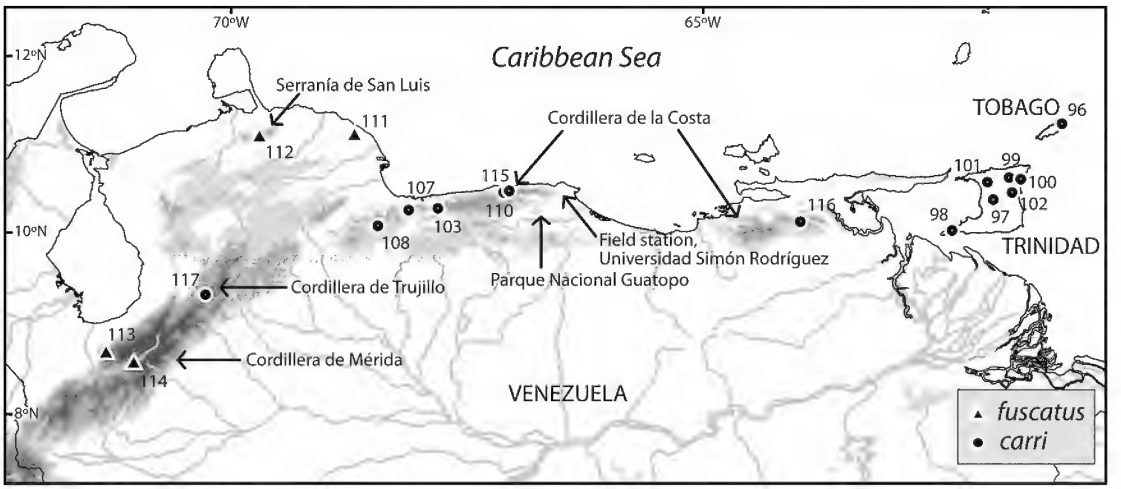

FIG. 17. Collecting localities of examined specimens of *Marmosops carri* and *M. fuscatus*. Numbers are keyed to entries in the gazetteer (appendix 1). Progressively darker shading indicates higher elevations: pale gray ≥500 m, medium gray ≥1000 m, dark gray ≥2000 m, darkest gray ≥3000 m.

our comparisons of representative specimens of these taxa.

Marmosops carri is substantially larger than *M. handleyi* in all external measurements, especially in three dimensions (HBL, LT, and Ear) that exhibit nonoverlapping variation in same-sex sample comparisons. In qualitative external comparisons, these species principally differ in coloration: whereas *M. carri* has grayish-brown dorsal body pelage and entirely white forefeet, *M. handleyi* has dark-brown dorsal pelage and dark metacarpals that contrast in color with its whitish manual digits. Skulls and dentitions of *M. carri* are considerably larger than those of *M. handleyi*, exhibiting nonoverlapping variation in same-sex comparisons of eight dimensions (CBL, ZB, PL, PB, MTR, LM, M1–3, and WM3). Overall, the skull of *M. carri* is more heavily built (especially in males) by comparison with the more delicate cranial construction of *M. handleyi*. In qualitative aspects of craniodental morphology, *M. carri* principally differs from *M. handleyi* by its uniformly narrow nasals (the nasals are posteriorly expanded in *M. handleyi*); unicuspid male C1 (this tooth has a posterior accessory cusp in male *M. handleyi*), and absence of a lingual accessory cusp on c1 in most specimens of both sexes (a lingual accessory cusp on c1 is present in both sexes of *M. handleyi*).

Marmosops carri is much larger than *M. invictus*, with no overlapping variation in same-sex comparisons of most measured dimensions. These species also differ strikingly in dorsal pelage coloration (much paler in *M. carri* than in *M. invictus*), coloration of the forefeet (entirely whitish in *M. carri*, whereas the metacarpals are dark in *M. invictus*), and tail markings (the tail is much more distinctly bicolored in *M. carri*). Qualitative craniodental comparisons reveal several additional contrasting differences. Among others, *M. carri* has uniformly narrow nasals, whereas the nasals are laterally expanded near the maxillary-frontal suture in *M. invictus*; at least the ventral lacrimal foramen is consistently visible in lateral view in *M. carri*, whereas this foramen is concealed inside the orbit in *M. invictus*; palatine fenestrae are often present in *M. carri*, whereas palatine perforations are consistently absent in *M. invictus*); c1 is a tall unicuspid tooth in male *M. carri*, whereas this tooth is short and premolariform in male *M. invictus*; and the m1 entoconid is subequal in height to the adjacent m2 paraconid in *M. carri*, whereas

the m1 entoconid is shorter than the m2 paraconid in *M. invictus*.

Remarks: *Marmosops carri* exhibits noteworthy sexual size dimorphism, with adult males averaging larger than adult females in most measured dimensions, especially those prone to strong positive allometry (e.g., zygomatic breadth; tables 5, 6). The sexes additionally differ in interorbital and canine morphology as described above. Maturational changes in the interorbital morphology of adult males appear to result from enlargement of the temporalis musculature, which is accommodated by an increasingly well-defined postorbital constriction and by supraorbital remodeling.

This species was long regarded (e.g., by Tate, 1933) as endemic to Trinidad, but Handley and Gordon (1979) correctly observed that specimens from the coastal cordilleras on the adjacent Venezuelan mainland are morphologically indistinguishable from Trinidadian material. Handley and Gordon recognized that specimens referable to *Marmosops carri* are distinctively larger than topotypical material of *Marmosops fuscatus* (from the Mérida Andes), but they judged these taxa to be conspecific and used the older name (*fuscatus*) for both.

Although *Marmosops carri* and *M. fuscatus* are morphologically similar (in particular, these are the only species of *Sciophanes* that exhibit large size and uniformly narrow nasals), they form distinct cytochrome-*b* haplogroups (Díaz-Nieto et al., 2016a), and measured specimens have nonoverlapping molar dimensions: LM = 7.0–7.7 mm in *M. carri* ($N = 28$) versus 6.0–6.7 mm in *M. fuscatus* ($N = 8$). The specimen from Trujillo (USNM 372934) that Handley and Gordon (1979) believed to be intermediate to *M. carri* and *M. fuscatus* has large molars (LM = 7.0 mm) and belongs to the same haplogroup that occurs on Trinidad (Díaz-Nieto et al., 2016a: fig. S1); therefore, we refer this specimen (and others collected in the Cordillera de Trujillo) to *M. carri*.

We have not examined any voucher material from two ecological studies of mouse opossums identified as *Marmosops fuscatus*, one by O'Connell (1979) and the other by Cordero (2001). O'Connell's study was carried out at Parque Nacional Guatopo in the interior coastal range of northern Venezuela (ca. 10°05′ N, 66°30′ W; on the border between the states of Miranda and Guárico), where "*M. fuscatus*" was said to occur only at higher elevations, presumably in premontane rain forest. Cordero's study was carried out at a field station of the Universidad Simón Rodríguez, close to the Caribbean coast in northern Venezuela (10°20′ N, 66°15′ W; in Miranda), where "*M. fuscatus*" was trapped in lowland rain forest near sea level. Based on their geographic locations (fig. 17), we expect that the species observed in both of these studies was *M. carri*. Also unexamined by us are a substantial number of Venezuelan specimens identified as *M. fuscatus* (see Pérez-Hernández, 1989), many of which seem likely to represent *M. carri*. A careful review of this and subsequently collected in-country material should contribute to a more accurate assessment of the geographic ranges of these taxa, and we encourage additional sequencing efforts to test the correlation between haplotype membership and morphometric divergence upon which our hypothesis of full species status is largely based.

Specimens examined ($N = 70$): **Trinidad and Tobago**—*Tobago,* near Charlotteville (AMNH 259970, 259978, 259979); *Trinidad,* Caparo (AMNH 7313/5921, 7314/5922), Cedros (AMNH 234951), Cumaca (AMNH 169759, 169760), Rio Grande Forest (AMNH 186437, 186438, 188353), St. Augustine (AMNH 150007), Turure Forest (AMNH 214439, 214441, 234952–234956, 234959, 234974). **Venezuela**—*Aragua,* Rancho Grande (AMNH 144832; USNM 517256–517260); *Carabobo,* 4 km NW Montalbán (USNM 418515, 443731, 443783–443789, 496520, 496521), Cumbre de Valencia (AMNH 31531); *Distrito Federal,* Los Venados (USNM 370022–370024); *Miranda/Vargas,* Hotel Humboldt (USNM 370027–370031, 370033–370039, 370041, 370042, 371300, 496517); *Monagas,* San Agustín (USNM 406925–406932, 4069324); *Trujillo*, 13–14 km E Trujillo (KU 120254, USNM 372933, 372934).

Marmosops fuscatus (Thomas, 1896)

Figures 4B, 15, 16

Marmosa fuscata Thomas, 1896: 313 (original description).

Didelphys (*Marmosa*) *fuscata:* Trouessart, 1898: 1240 (name combination).

Marmosa (*Marmosa*) *fuscata:* Cabrera, 1919: 36 (name combination).

Marmosa cracens Handley and Gordon, 1979: 66 (original description). Type locality "near La Pastora, 14 km ENE Mirimire, Falcón, Venezuela."

Marmosa crascens: Reig et al., 1985: 342 (incorrect subsequent spelling of *M. cracens* Handley and Gordon, 1979).

Marmosops cracens: Gardner and Creighton, 1989: 4 (name combination).

Marmosops fuscatus: Gardner and Creighton, 1989: 4 (first use of current binomial).

Marmosa (*Marmosops*) *cracens:* Pérez-Hernández et al., 1994: 35 (name combination).

Marmosa (*Marmosops*) *fuscata:* Pérez-Hernández et al., 1994: 37 (name combination); part (not including misidentified specimens of *M. carri*).

Marmosops fuscatus fuscatus: Gardner and Creighton, 2008: 66 (name combination); part (not including misidentified specimens of *M. carri*).

Type material: The holotype (by original designation) consists of the skin and skull of an old adult female (BMNH 1896.11.1.6) collected by "S. Briceno" (= Salomón Briceño-Gabaldón, a commercial collector) at 1630 m elevation along the Río Albarregas (misspelled "Abbaregas" by Thomas, 1896) near the city of Mérida (fig. 17: locality 114) in the Venezuelan state of Mérida on 6 April 1896.

Distribution, habitats, and sympatry: Examined specimens of *Marmosops fuscatus* are from four Venezuelan localities, two in the Mérida Andes (Cordillera de Mérida), one in the Serranía de San Luis of western Falcón, and one in the Caribbean coastal lowlands of eastern Falcón (fig. 17). Although recorded elevations range from 125 to 2350 m above sea level, capture habitats seem to be either premontane or montane rain forest.[6] Previous reports of this species from Colombia (e.g., Gardner and Creighton, 2008: map 28) were based on misidentified material (see Remarks, below). *Marmosops fuscatus* is not known to occur sympatrically with any congeneric species, although it could be expected to do so with *M. carri* and *M. ojastii*, which have adjacent or overlapping geographic ranges.

Description: Body pelage dark grayish brown (near Sepia) middorsally, indistinctly paler laterally, and about 7–9 mm long at midback (shorter in specimens from lower elevations than in those from the Mérida Andes); ventral pelage superficially whitish but uniformly gray based except for the apex of the chin, oral margins, and scrotum (which are covered with self-whitish hairs). (One examined specimen, AMNH 276509, has small patches of self-white hairs along the inner thighs.) Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting in color with the digits); lateral carpal tubercles bladelike in all examined adult males. Mammary formula unknown. Tail longer than combined length of head and body (mean LT/HBL × 100 = 110%); dorsal caudal surface dark, but indistinctly paler distally in some specimens; ventral surface distinctly paler.

Nasal bones long (extending well behind the lacrimals) and uniformly narrow (without distinct lateral expansion at the maxillary-frontal suture). Interorbital region broad, with rounded supraorbital margins in females and young adult males, but relatively narrower and tending to develop squared supraorbital margins in large adult males; postorbital processes absent or

[6] Handley and Gordon (1979) reported that the type series of *Marmosa cracens* was collected between 125 and 170 m above sea level on "the steep, moist, north slope of an isolated, low mountain" near the Caribbean coast. Vegetation of distinctly montane character can extend downslope to within 100 m above sea level on such isolated peaks, which intercept moisture-laden sea breezes and are often shrouded in low-lying clouds. The cloud forest (montane rain forest) vegetation at capture localities in the Serranía de San Luis was briefly described by Anderson et al. (2012).

indistinct. Lacrimal foramina variable (the upper foramen is usually not visible in lateral view, but the lower foramen can be either laterally visible or concealed inside the anterior orbital margin);[7] zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae present or absent (when present these can appear as a single small perforation on each side or as several small irregular perforations on both sides). Dorsolateral margin of ethmoid foramen usually formed by the frontal.

Upper canine (C1) sexually dimorphic (longer and unicuspid in males, shorter and with posterior accessory cusp in young female specimens with unworn teeth). Upper third molar (M3) anterolabial cingulum discontinuous with preprotocrista (anterior cingulum incomplete). Lower canine (c1) sexually dimorphic (erect, without a posterior accessory cusp, and taller than p1 in males versus procumbent, with a posterior accessory cusp, and subequal in height to p1 in females); c1 anterolingual accessory cusp usually absent in both sexes. Entoconid of m1 subequal in height to adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

Comparisons: Comparisons between *Marmosops fuscatus* and *M. carri* have already been described (see above).

Marmosops fuscatus is substantially larger than *M. handleyi* in head-and-body length and has a proportionately shorter tail (tables 5, 6). Externally the two species differ in the same characters that distinguish *M. carri* from *M. handleyi*, namely dorsal pelage coloration (dark grayish brown in *fuscatus*, dark brown in *handleyi*) and forefoot coloration (the manus is entirely whitish in *fuscatus*, whereas the pale digits contrast with the dark metacarpals in *handleyi*). *Marmosops fuscatus* also averages larger than *M. handleyi* in most craniodental dimensions, including four measurements (CBL, ZB, PL, MTR, and WM3) that exhibit nonoverlapping variation in same-sex comparisons. These species also differ in some of the same qualitative craniodental characters that distinguish *M. carri* and *M. handleyi*; in particular, *M. fuscatus* has much narrower nasals than *M. handleyi* (in which these bones are conspicuously expanded laterally at the maxillary-frontal suture), and males of *M. fuscatus* have unicuspid C1 and c1, whereas these teeth consistently have a small posterior accessory cusp in males of *M. handleyi*. Additionally, the dorsolateral margin of the ethmoid foramen is usually formed by the frontal in *M. fuscatus*, whereas the dorsolateral margin of this foramen is formed by the orbitosphenoid in *M. handleyi*. Lastly, the distinct lingual accessory cusp of c1 that appears to be consistently present in *M. handleyi* is absent in *M. fuscatus*.

Marmosops fuscatus is substantially larger than *M. invictus* in all external dimensions. In qualitative external characters, *M. fuscatus* is most readily distinguished from *M. invictus* by its paler dorsal coloration (the dorsal pelage of *invictus* is consistently much darker), by its entirely pale forefeet (the metacarpals are dark in *M. invictus*), and by its more distinctly bicolored tail (the tail is only indistinctly paler ventrally than dorsally in *M. invictus*). *Marmosops fuscatus* averages larger than *M. invictus* in most craniodental dimensions, including five measurements (CBL, NL, ZB, PL, MTR) that exhibit nonoverlapping variation in same-sex comparisons. Craniodental qualitative differences between these quite dissimilar species include the shape of the nasals (uniformly narrow in *M. fuscatus*, laterally expanded in *M. invictus*), dorsolateral margin of the ethmoid foramen (usually formed by the frontal in *M. fuscatus*, by the orbitosphenoid in *M. invictus*), C1 posterior accessory cusp (absent in males of *M. fuscatus*, present in both sexes of *M. invictus*), M3 anterior cingulum (incomplete in *M. fuscatus*, narrowly complete in *M. invictus*), c1 morphology (erect and unicuspid in male *M. fuscatus*, procumbent and premolariform in *M. invictus*), c1 lingual accessory cusp

[7] The lower lacrimal foramen is laterally visible in some specimens (e.g., BMNH 3.1.5.2, 3.1.5.3, FMNH 22174, USNM 442719) but not in others (e.g., AMNH 276580, 276509). The specimens in which this foramen is visible are the largest in overall size and have the most heavily ossified skulls, but we lack sufficient material to determine whether or not this trait is age correlated.

(absent in *M. fuscatus*, usually present in *M. invictus*), and m1 entoconid (subequal to adjacent m2 paraconid in *fuscatus*, shorter than m2 paraconid in *M. invictus*).

Remarks: *Marmosa perfusca*, a nominal species that Thomas (1924) described from the Cordillera Oriental of Colombia, was synonymized with *M. fuscatus* by Tate (1933: 173), and some authors (e.g., Gardner and Creighton, 2008: 66) have treated it as a valid subspecies ("*Marmosops fuscatus perfuscus*"). However, the type of *perfusca* (BMNH 1923.11.13.18, consisting of the skin and skull of an old adult female) has posteriorly widened nasals, a short subsquamosal foramen (not exposing the petrosal behind the sulcus of the prootic sinus), and only one antebrachial vibrissa. In these and other characters it closely resembles *Marmosops caucae* (Thomas, 1900), a member of the nominotypical subgenus of *Marmosops*. A second Colombian specimen that Tate (1933) referred to *Marmosa fuscata* is AMNH 34641, also from the Cordillera Oriental;[8] like BMNH 1923.11.13.18, this specimen appears to represent *M. caucae*. To the best of our knowledge, there are no valid records of *Marmosops fuscatus* from Colombia.

Handley and Gordon (1979: 67) described *Marmosa cracens* as "in almost every respect of pelage and skull character ... a miniature replica of *M. fuscata*, distinguishable from it only by its small size and the short, broad shape of its palate." Indeed, the male holotype of *cracens* (USNM 418503) is substantially smaller than any adult male specimen of *Marmosops fuscatus* that we measured. For example, the condylobasal length of the skull of USNM 418503 is 28.4 mm, whereas the range of condylobasal lengths of five adult male *M. fuscatus* is 31.8–35.4 mm. However, this size difference is plausibly explained by ontogeny: the type series of *cracens* consists of subadults (with incompletely erupted P3s), not young adults (contra Handley and Gordon, 1979). The subadult holotype and paratype of *cracens* do have relatively wider palates (PB/PL = 0.57–0.59) than topotypical adult *fuscatus* (0.51–0.53), but relative width of the palate is another ontogenetically variable trait because didelphid palates become proportionately longer and narrower with advancing age (Abdala et al., 2001). Lastly, we (Díaz-Nieto et al., 2016a) amplified partial (579–619 bp) cytochrome-*b* sequences from the holotype and a paratype of *cracens*, which differ by only 2.2% (uncorrected) from a partial (1008 bp) cytochrome-*b* sequence that we amplified from a topotype of *M. fuscatus* (BMNH 1903.1.5.2). Because this genetic distance is well within the range of values commonly obtained from comparisons of conspecific sequences of other mammals, and because the phenotypic differences that Handley and Gordon (1979) alleged between *cracens* and *fuscatus* seem to be attributable to the immaturity of their type series, we treat the former as a subjective junior synonym.

Specimens examined (N = 8): **Venezuela**—*Falcón,* Near La Pastora (USNM 418503 [holotype of *cracens*], 442719), Serranía de San Luís (AMNH 276509, 276580); *Mérida,* La Azulita (FMNH 22174), Mérida (BMNH 1896.11.1.6 [holotype], 1903.1.5.2, 1903.1.5.3).

Marmosops handleyi (Pine, 1981)

Figures 2, 18, 19

Marmosa handleyi Pine, 1981: 67 (original description).

Marmosops handleyi: Gardner and Creighton, 1989: 4 (first use of current binomial).

Type material: The holotype (by original designation) consists of the skin, skull, and postcranial skeleton of an adult female (FMNH 69838; original number PH 4371) collected by Philip Hershkovitz at a site 9 km south of Valdivia (fig. 20: locality 24) in the Colombian

[8] This specimen was collected by G. O'Connell on 4 April 1913 at "El Roble," a locality that Tate (1933: 173) erroneously placed in Departamento Cauca and that Gardner and Creighton (2008: 66) located in Departamento Quindío (on the western slope of the Cordillera Central; Paynter, 1997). However, Geoffroy O'Connell was a member of the 1913 AMNH expedition that worked at a different place called El Roble, "a posada on the trail from Bogotá to Fusugasugá [= Fusagasugá]" on the western slope of the Cordillera Oriental (Chapman, 1917: 645); according to Paynter (1997), this locality is near 4°23′N, 74°19′W.

department of Antioquia at an elevation of 1400 m on 16 June 1950. In addition, Pine's (1981) original material included an adult male paratype (FMNH 70926).

Distribution, habitats, and sympatry: Examined specimens of *Marmosops handleyi* are all from the northern terminus of the Cordillera Central (central Andes) of Colombia, where they have been collected in humid premontane and montane rain forest at elevations ranging from 1400 to 1950 m (fig. 20). This species has been collected sympatrically with *M. chucha* (a new species of the Bishopi Group; see below) and with *M. caucae* (a member of the nominotypical subgenus; Díaz-N. et al., 2011).

Description: Body pelage dark brown to chestnut brown middorsally, indistinctly paler laterally, about 9–10 mm long at midback, and somewhat woolly in texture; ventral pelage superficially whitish, but hairs of throat, chest, and abdomen uniformly gray based (only the apex of the chin, the oral margins, the scrotum, and mammary region consistently have self-white fur).[9] Metacarpals covered dorsally with dark hairs (contrasting in color with the pale manual digits); lateral carpal tubercles bladelike. Mammary formula 3–1–3 = 7 in all examined females with conspicuous teats. Tail longer than combined length of head and body (mean LT/HBL × 100 = 125%), dorsal caudal surface dark gray but somewhat paler distally; ventral caudal surface distinctly paler.

Nasal bones long (extending well behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Upper lacrimal foramen not visible in lateral view, but lower foramen laterally exposed; zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae present (usually as a pair of large rounded perforations). Dorsolateral margin of ethmoid foramen with equal contribution of frontal and orbitosphenoid.

Upper canine (C1) short in both sexes but sexually dimorphic in shape: male C1 with posterior accessory cusp only, female C1 with both anterior and posterior accessory cusps. Upper third molar (M3) anterolabial cingulum discontinuous with preprotocrista (anterior cingulum incomplete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp present. Entoconid of m1 subequal in height to adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

Comparisons: Comparisons of *Marmosops handleyi* with *M. carri* and *M. fuscatus* have already been described (see above).

Although *Marmosops handleyi* averages slightly larger than *M. invictus* in most same-sex comparisons of external dimensions (tables 5, 6), sample sizes for both species are small, and it seems unlikely that any external measurement will prove to be diagnostic as more material becomes available. A more consistent external difference between these species is pelage color (distinctly brownish in *handleyi* versus dark grayish brown to blackish gray in *invictus*) and fur length (9–10 mm middorsally in *handleyi* versus 6–7 mm in *invictus*). The two species broadly overlap in craniodental measurements, none of which, therefore, is useful for identification. Instead, *M. handleyi* is more readily distinguished from *M. invictus* by the consistent presence of palatine fenestrae (consistently absent in *M. invictus*), by the presence of both anterior and posterior accessory C1 cusps in females (females usually have only a posterior accessory C1 cusp in *M. invictus*), by lacking a complete M3 anterior cingulum (M3 has a narrowly complete anterior cingulum in *M. invictus*), and by having an m1 entoconid that is subequal in height to the adjacent m2 paraconid (the m1 entoconid is shorter than the m2 paraconid in *invictus*).

Remarks: *Marmosops handleyi* had not been collected for 60 years before it was rediscovered and redescribed by Díaz-N. et al. (2011), whose report should be consulted for additional mor-

[9] Pine (1981: 68) described the dorsal pelage as "fuscous," a grayer shade than we observed in fresh skins. Unfortunately, none were compared by us with color swatches in Ridgway (1912). One specimen (CTUA 415, a subadult male) has a 5 × 15 mm midventral streak of self-white abdominal hairs.

FIG. 18. Dorsal and ventral views of skulls of *Marmosops handleyi* (left, CTUA 411) and *M. invictus* (right, USNM 337962). All views about ×3.

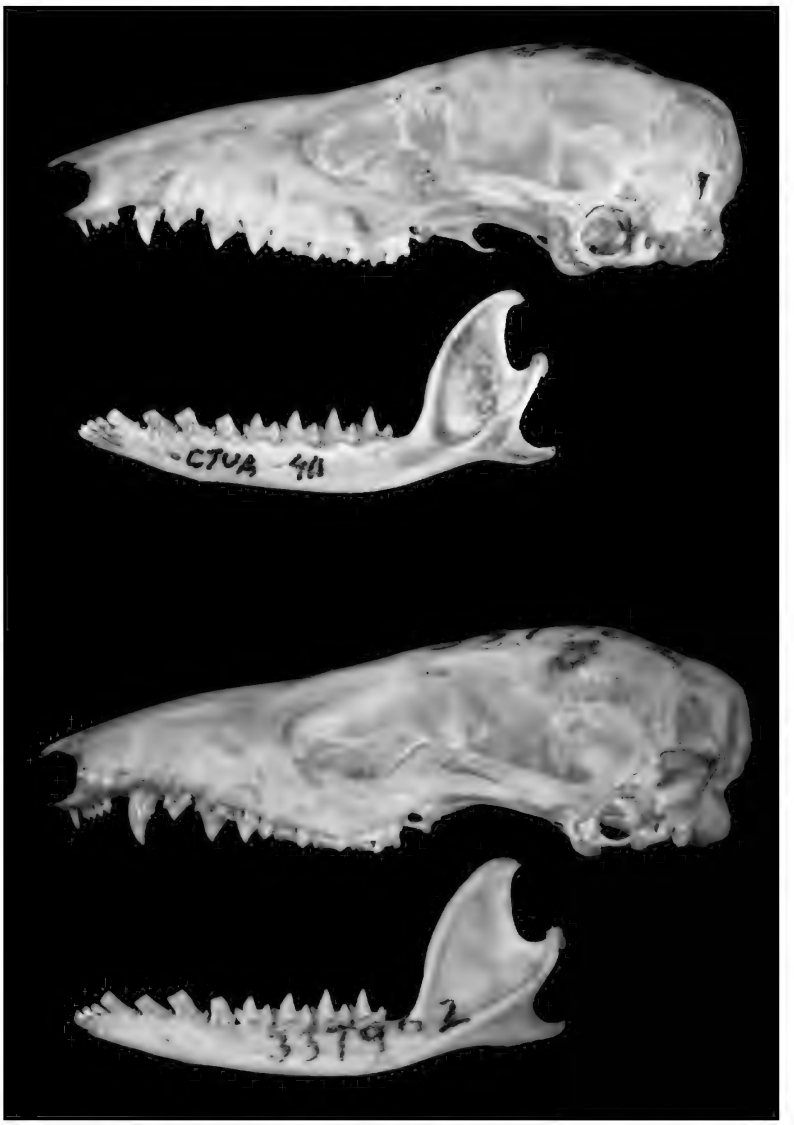

FIG. 19. Lateral views of skulls and mandibles of *Marmosops handleyi* (above, CTUA 411) and *M. invictus* (below, USNM 337962). All views about ×3.

phological, geographical, and ecological information. Using the dichotomous key in Gardner and Creighton (2008), this species would be misdidentified as *M. juninensis.*

SPECIMENS EXAMINED (N = 10): **Colombia—** *Antioquia,* Finca Costa Rica (CTUA 410–412, 433); Finca El Bosque (CTUA 413, 414), Finca Villa Nueva (CTUA 415, 416), 9 km S Valdivia (FMNH 69823, 69838).

Marmosops invictus (Goldman, 1912)

Figures 4A, 18, 19

Marmosa invicta Goldman, 1912: 3 (original description).

Didelphis (Marmosops) invicta: Matschie, 1916: 270 (name combination).

Marmosops invictus: Gardner and Creighton 1989: 4 (first use of current binomial).

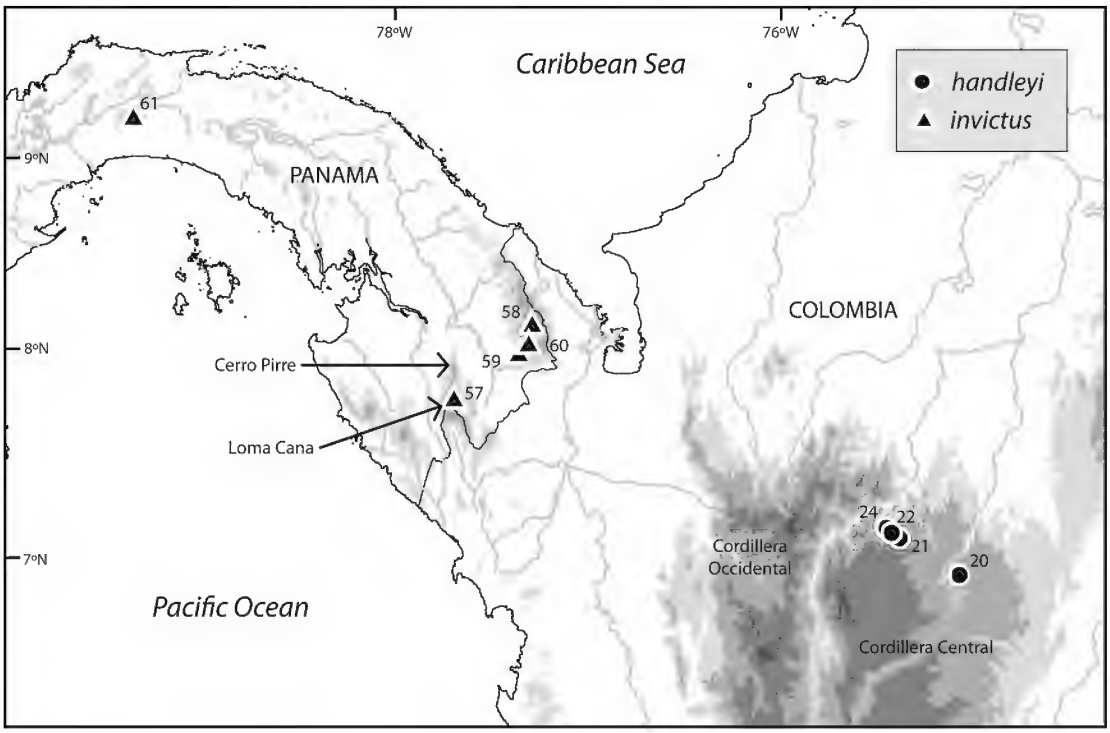

FIG. 20. Collecting localities of examined specimens of *Marmosops handleyi* and *M. invictus*. Numbers are keyed to entries in the gazetteer (appendix 1). Progressively darker shading indicates higher elevations: pale gray ≥500 m, medium gray ≥1000 m, dark gray ≥2000 m, darkest gray ≥3000 m.

Type material: The holotype (by original designation) consists of the skin and skull of an adult male (USNM 178708; original number 21517) collected by E.A. Goldman at Cana (fig. 20: locality 57), in Darién province, Panama, on 14 March 1912. In addition to the holotype, Goldman's original material included an adult female paratype (USNM 178709).

Distribution, habitats, and sympatry: Examined specimens of *Marmosops invictus* are all from eastern Panama with recorded elevations between 600 and 1500 m above sea level (fig. 20). Handley (1966), who may have examined more material than we have seen, gave the elevational range as ca. 450–1200 m and remarked that the species might occur throughout Panama in suitable habitat. Although the lower elevations at which this species occurs would support lowland rain forest in Amazonia, humid forests of distinctly montane character (e.g., those at the type locality; Goldman, 1920: figs. 1, 2) can be found well below 1000 m on the low mountains and foothills of Central America (Myers, 1969). Premontane rain forest seems likely to be the usual habitat of this species, which is not known to occur sympatrically with any other species of the subgenus *Sciophanes*. However, *M. caucae*, a member of the nominotypical subgenus, occurs at elevations >1400 m in the Darién highlands of eastern Panama (Loma Cana and Cerro Pirre) and probably coexists with *M. invictus* in some places.

Description: Dorsal body pelage uniformly dark grayish brown to blackish gray (near Bone Brown to Blackish Brown)—not appreciably paler laterally—and only about 6–7 mm long at midback; ventral fur silvery gray (the hairs with dark-gray bases and whitish tips) over throat, chest, and abdomen (only the chin, oral margins, and groin have self-white fur). Manus with dark

fur over all or part of metacarpals (contrasting in color with whitish digits); lateral carpal tubercles bladelike. Mammae 3–1–3 = 7 in all examined females with visible teats. Tail longer than combined length of head and body (mean LT/HBL × 100 = 122%); dorsal caudal surface dark gray from base to tip; ventral caudal surface indistinctly paler in some specimens (e.g., USNM 306386), almost as dark as dorsal surface in others (e.g., USNM 309265).

Nasal bones long (extending well behind the lacrimals in most specimens) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae absent (but some specimens have minute palatine perforations on one or both sides). Dorsolateral margin of ethmoid foramen formed by the orbitosphenoid.

Upper canine (C1) short, usually with posterior accessory cusps in male and female specimens (two females—USNM 178709, 306386—have indistinct anterior accessory C1 cusps, and the holotype completely lacks accessory cusps). Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp usually present. Entoconid of m1 subequal in height to adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

Comparisons: Comparisons of *Marmosops invictus* with other members of the Fuscatus Group have already been described (see above).

Remarks: All of the material we examined for this revision was collected >50 years ago, and we are not aware of any recently collected specimens. However, Mangan and Adler (2000) reported trapping *Marmosops invictus* in the course of an ecological study in western Panama, well outside the specimen-documented range of this species. In the absence of voucher material, the identity of the animals they trapped and released remains to be determined.

In a recent discussion of cytochrome oxidase subunit I (COI) barcoding results, Lim (2012) reported the occurrence of *Marmosops invictus* in Panama and Ecuador, but the specimens he sequenced (ROM 116281, 118844, and F41897)[10] appear to have been misidentified. We examined the Panamanian specimen (ROM 116281), which consists of a skin and skull with all the diagnostic attributes of the nominotypical subgenus, not *Sciophanes*. In addition, its teeth are larger than those of any measured specimen of *M. invictus* (e.g., LM = 6.8 mm versus 6.0–6.5 mm), its ventral pelage includes a median streak of self-white fur, and it has well-developed palatine fenestrae. In these and other traits ROM 116281 resembles numerous specimens of a widespread species (or species complex) for which *M. caucae* is the oldest available name, and the cytochrome-*b* sequence that we (Díaz-Nieto et al., 2016a) obtained from ROM 116281 also unequivocally associates this specimen with the *M. caucae* complex. The two Ecuadorean specimens (ROM 118844, F41897) cannot be found at present (Jacqueline Miller, personal commun.), but as their COI barcodes clustered with the barcode obtained from ROM 116281, it seems likely that they are also members of the *M. caucae* complex, which is abundantly represented among other sequenced Ecuadorean material (Díaz-Nieto et al., 2016a).

Specimens examined (N = 10): **Panama—** *Darién,* Cana (USNM 178708 [holotype], 178709), Cerro Tacarcuna (USNM 337959–337962), Tacarcuna Casita Camp (USNM 309265), Tacarcuna Laguna Camp (USNM 309266, 309267); *Panamá,* Cerro Azul (USNM 306386).

Species of the Bishopi Group

Species of the *Marmosops bishopi* group are distinguished from other members of the subgenus *Sciophanes* by their extensively self-white ventral

[10] Corresponding to records ABSMS616-06, ABECB166-08, and ABRMM151-07 in the Barcode of Life Data system (www.boldsystems.org; accessed in January 2016).

fur (except *M. juninensis*), bladelike lateral carpal tubercles, 4–1–4 = 9 mammae, narrowly complete M3 anterior cingulum, and an m1 entoconid that is shorter than the adjacent m2 paraconid. This clade is widely distributed in western Amazonia, along the eastern slopes of the Peruvian Andes, in northern Colombia, and in northwestern Venezuela. Diagnostic quantitative and qualitative comparisons are summarized in tables 8–10.

Marmosops bishopi (Pine, 1981)

Figures 3B, 8A, 21, 22, 23A

Marmosa parvidens bishopi Pine, 1981: 63 (original description).

Marmosops parvidens bishopi: Gardner, 1993: 20 (name combination).

Marmosops bishopi: Voss et al., 2001: 48 (first use of current binomial).

Type material: The holotype (by original designation) consists of the skin and skull of an adult female (USNM 393535; original number RHP 5157) collected by Ronald H. Pine near the base camp of the Royal Geographical Society's Xavantina-Cachimbo expedition, 264 km N (by road) Xavantina in the Serra do Roncador, Mato Grosso, Brazil (fig. 24: locality 12). Although Pine (1981) did not examine any other referred material, he mentioned two topotypical BMNH specimens that we have been unable to locate.

Distribution, habitats, and sympatry: Examined specimens that we refer to *Marmosops bishopi* are from the western Amazonian lowlands of southeastern Colombia, eastern Ecuador, eastern Peru, northeastern Bolivia, and western Brazil; the eastern Andean foothills of Peru and Bolivia; and the Cerrado of central Brazil and eastern Bolivia (fig. 24). The species has been collected from gallery forest in savanna-dominated landscapes (e.g., at the Serra do Roncador; Ratter et al., 1973; Eiten, 1975), in lowland rainforest (Patton et al., 2000; Hice and Velazco, 2012), and in premontane rain forest. Recorded elevations range from 100 to 1300 m. Not surprisingly, the broad geographic range of *M. bishopi* overlaps those of several congeneric species. Among other reports of sympatry, this species has been collected together with *M. juninensis* (in eastern Peru; Peralta and Pacheco, 2014); *M. noctivagus*, *M. caucae*, and an undescribed species (in western Brazil; Patton et al., 2000); and *M. ocellatus* (in eastern Bolivia; Emmons et al., 2006).

Description: Dorsal body pelage geographically variable, but usually some shade of grayish brown (near Bister) middorsally,[11] often indistinctly paler laterally, and about 7–9 mm at midback; ventral pelage predominantly self-white from chin to groin (including the inside surfaces of the fore- and hind limbs), with or without narrow lateral borders of gray-based abdominal fur. Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercles bladelike. Mammae 4–1–4 = 9 in all examined females with visible teats. Tail substantially longer than combined length of head and body (mean LT/HBL × 100 = 130%); often indistinctly bicolored (dark above, somewhat paler below), but unicolored-dark in some specimens (e.g., AMNH 276723) and distinctly bicolored in others (e.g., USNM 584464).

Nasals proportionately shorter than in species of Parvidens and Fuscatus groups (often not extending behind lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina usually concealed from lateral view inside anterior orbital margin (but in some specimens—e.g., AMNH 67243, KU 157970, MUSM 23803—the lower foramen is partially exposed in lateral view); zygomatic process of the squamosal broadly overlapped dorsally by jugal. Distinct palatine fenestrae absent (but a few specimens have minute palatine perforations on one or both sides). Dorsolateral margin of ethmoid foramen formed by the frontal.

[11] Cerrado specimens (e.g., USNM 393535, 584464) are paler (near Snuff Brown) than those from lowland rain forest, and a few specimens (e.g., FMNH 84251) are distinctly reddish (near Cinnamon Brown).

TABLE 8

Measurements (mm) and Weights (g) of Adult Male Specimens of the Bishopi Group of *Marmosops* (*Sciophanes*)

	M. bishopi[a]	*M. juninensis*[b]	*M. ojastii*[c]	*M. chucha*[d]	*M. magdalenae*[e]
HBL	103 (93–111) 20	98	94 (90–97) 2	105 (99–109) 5	103 (99–106) 2
LT	141 (126–153) 21	135	134 (130–138) 2	137 (134–141) 5	129 (125–132) 2
HF	17 (15–19) 19	17 (16–18) 2	18 (17–18) 2	18 (17–19) 5	18 (17–18) 2
Ear	21 (18–23) 20	21 (20–21) 2	20 (19–22) 2	21 (20–21) 4	19 (18–19) 2
CBL	28.3 (26.4–29.8) 20	27.7	25.8 (25.3–26.3) 2	28.9	28.3 (27.3–28.9) 3
NL	13.1 (12.2–13.9) 17	—	—	13.4 (13.3–13.6) 2	13.1 (12.5–13.9) 3
NB	3.6 (3.2–4.1) 24	3.7 (3.6–3.7) 2	3.0 (2.9–3.2) 2	3.9 (3.8–3.9) 2	3.8 (3.7–3.8) 3
LIB	5.6 (5.1–6.0) 24	5.6 (5.6–5.7) 2	5.3 (5.3–5.3) 2	5.6 (5.5–5.9) 4	5.5 (5.5–5.6) 3
ZB	14.7 (13.7–15.6) 24	13.9 (13.8–14.1) 2	13.6 (13.3–13.8) 2	15.2	15.1 (14.8–15.5) 3
PL	15.8 (14.6–16.8) 22	15.8	14.2 (13.8–14.7) 2	15.8 (15.7–15.9) 2	15.6 (14.9–16.0) 3
PB	8.6 (8.0–9.0) 24	8.3 (8.3–8.3) 2	8.2 (8.2–8.3) 2	8.9 (8.8–9.0) 2	8.7 (8.5–8.8) 3
MTR	11.5 (10.6–12.0) 24	11.3 (11.2–11.4) 2	10.6 (10.5–10.8) 2	11.4 (10.9–11.7) 3	11.3 (10.8–11.6) 3
LM	5.9 (5.4–6.3) 24	5.8 (5.7–5.8) 2	5.6 (5.6–5.6) 2	5.9 (5.7–6.1) 4	6.0 (5.9–6.1) 3
M1–3	5.1 (4.8–5.4) 24	5.0 (4.9–5.1) 2	5.0 (4.9-5.0) 2	5.2 (5.1–5.3) 4	5.2 (5.1–5.2) 3
WM3	1.9 (1.8–2.1) 24	1.8 (1.8–1.8) 2	1.8 (1.8–1.9) 2	1.9 (1.7–2.0) 4	1.9 (1.9–2.0) 3
Weight	25 (18–34) 16	—	—	26 (25–26) 2	24

[a] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 276700, 276705; CBF 7531; EPN 127, 10706; FMNH 84251, 169802, 203328, 203509; ICN 18338; KU157969; MSB 55843; MUSM 16237, 16240, 16803, 17691, 17723, 17930; MVZ 168966; QCAZ 10308; TTU 99031, 99032, 101239; USNM 584464.

[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 230014, 230016.

[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: EBRG 27474, 29540 (data from García et al., 2014); USNM 371299.

[d] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: FMNH 69825, 70925, 70927; MHNUC 986, MHNUC uncataloged (DCV069).

[e] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: FMNH 70926; ICN 18788, ICN uncataloged (YMS1820).

Upper canine short and sexually dimorphic (males with posterior accessory cusp only, females with both posterior and anterior accessory cusps). Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent. Entoconid of m1 shorter (sometimes much shorter) than adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

Comparisons: *Marmosops bishopi* overlaps broadly in all measured external and craniodental dimensions with *M. juninensis*, from which it cannot be distinguished morphometrically (tables 8, 9). Similarly, the coloration of the dorsal pelage offers no useful criterion for identifying these species due to the wide variation in this trait observed in *M. bishopi*. By contrast, the ventral pelage is taxonomically diagnostic: whereas a broad zone of self-white fur extends continuously from chin to anus, including the inside surfaces of the fore- and hind limbs in *M. bishopi*, the ventral fur of *M. juninensis* is almost entirely gray based (including the insides of the fore- and hind limbs), with only a narrow, discontinuous midventral streak of self-white fur in some specimens. Additionally, *M. bishopi* can be distinguished from *M. juninenis* by having the

TABLE 9

Measurements (mm) and Weights (g) of Adult Female Specimens of the Bishopi Group of *Marmosops* (*Sciophanes*)[a]

	M. bishopi[b]	*M. juninensis*[c]	*M. chucha*[d]	*M. magdalenae*[e]
HBL	101 (90–114) 7	104 (96–110) 3	100 (90–112) 4	99 (99) 2
LT	129 (116–141) 7	131 (122–137) 3	126 (119–133) 4	130 (129–130) 2
HF	16 (15–18) 8	16 (14–18) 3	16 (13–17) 4	17 (17) 2
Ear	20 (18–22) 8	19 (17–20) 2	19 (18–20) 4	20 (20) 2
CBL	27.5 (26.6–29.6) 9	28.3	27.2 (26.9–27.6) 3	27.1 (26.9–27.3) 2
NL	12.2 (11.7–13.1) 3	13.1 (13.0–13.3) 2	12.4 (11.7–12.7) 4	12.7 (12.5–12.8) 2
NB	3.5 (3.2–3.8) 11	3.4 (3.3–3.4) 2	3.5 (3.4–3.6) 4	3.7
LIB	5.4 (5.1–5.6) 11	5.7 (5.6–5.9) 3	5.4 (5.4–5.5) 4	5.5 (5.4–5.5) 2
ZB	14.6 (13.4–15.5) 11	14.2 (13.9–14.5) 2	14.4 (14.2–14.5) 2	14.8
PL	15.3 (14.7–16.3) 9	15.8 (15,7–16.0) 2	15.2 (14.9–15.4) 3	14.9 (14.9) 2
PB	8.8 (8.4–9.3) 10	8.6 (8.3–8.9) 3	8.4 (8.3–8.5) 3	8.8 (8.7–8.8) 2
MTR	11.4 (11.0–11.8) 11	11.4 (11.1–11.7) 3	11.2 (10.9–11.6) 4	10.9 (10.8–11.1) 2
LM	5.9 (5.6–6.1) 11	5.9 (5.6–6.0) 3	5.8 (5.5–6.0) 4	5.8 (5.8–5.9) 2
M1–3	5.1 (4.8–5.3) 11	5.1 (4.9–5.2) 3	5.0 (4.8–5.2) 4	5.1 (5.1–5.2) 2
WM3	2.0 (1.8–2.1) 11	1.9 (1.8–2.1) 3	1.9 (1.8–2.0) 4	2.0 (1.9–2.0) 2
Weight	21 (17–29) 5	27	18	—

[a] We have not examined any female specimen of *Marmosops ojastii*; according to García et al. (2014), adult female specimens of *M. ojastii* are unknown.
[b] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 268938; MUSM 17661, 23802, 24432, 33487; QCAZ 8168, 8169; TTU 98964, 101238, 101257; USNM 393535.
[c] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: AMNH 63864; 230015; MUSM 40617.
[d] The mean, the observed range (in parentheses), and the sample size are provided for each measurement of the following series: CTUA 434; FMNH 69822, 69837, 70928.
[e] Measurement of the following specimen: ICN 19924.

zygomatic process of the squamosal broadly overlapped dorsally by the jugal (the zygomatic process of the squamosal is not or is only slightly overlapped by the jugal in *M. juninensis*; fig. 23), by having unfenestrated palatines (palatine fenestrae are consistently present in *M. juninensis*), and by lacking a c1 anterolingual accessory cusp (c1 usually has a small anterolingual accessory cusp in *M. juninensis*).

Marmosops bishopi is substantially larger, on average, than *M. ojastii* in head-and-body length and in many craniodental measurements, but these morphometric comparisons need to be interpreted cautiously because only two adult males of *M. ojastii* have been measured, and one of these (USNM 371299) is quite young. The dorsal pelage of the single skin of *M. ojastii* that we examined (USNM 371299) is somewhat paler than is usual in *M. bishopi*, but this contrast does not seem to be consistent with pelage color descriptors used by García et al. (2014: table 2). Instead, those authors distinguished *M. bishopi* from *M. ojastii* based on several other characters, including the size and shape of the lateral carpal tubercle (said to be larger and more flattened in *M. bishopi* versus smaller and triangular in *M. ojastii*), size and position of the hypothenar pad of the manus (said to be larger than the interdigital pads in *M. bishopi* versus smaller than the interdigitals in *M. ojastii*), position of the lacrimal foramina (said to be exposed outside the orbit in *M. bishopi* versus concealed from lateral

TABLE 10

Diagnostic Comparisons among Members of the Bishopi Group of *Marmosops* (*Sciophanes*)

Character	*M. bishopi*	*M. juninensis*	*M. ojastii*	*M. chucha*	*M. magdalenae*
Distribution	cis-Andean	Andean	trans-Andean	trans-Andean	trans-Andean
Self-white ventral fur	broad	absent/ discontinuous	broad	broad	broad
Squamosal-jugal overlap	broad	shallow/absent	broad	broad	broad
Palatine fenestrae	usually absent	large/multiple	absent	absent	large
C1 accessory cusps	♂: posterior only	♂: posterior only	♂: posterior only	♂: posterior only	♂: posterior only
	♀: variable[a]	♀: posterior only	♀: posterior only[b]	♀: anterior & posterior	♀: posterior only

[a] All females have a posterior accessory cusp, but some also have an anterior accessory cusp.
[b] We did not examine females of this species, but García et al. (2014) described juvenile females with posterior accessory cusps.

view inside the orbit in *M. ojastii*), development of lambdoid crests on the occiput (said to be larger in *M. bishopi* than in *M. ojastii*), position of the posterolateral palatal foramina (said to be larger and to extend anteriorly to the protocone of M4 in *M. bishopi* versus smaller and not extending anteriorly to the protocone of M4 in *M. ojastii*), and width of the masseteric fossa of the mandible (said to differ in some undefined way between these species). Although our observations (based on USNM 371299) are not entirely consistent with García et al.'s (2014), we have not examined their type material. The only other potentially diagnostic character we noted is the dorsolateral margin of the ethmoid foramen, which is usually formed by the frontal in *M. bishopi*, whereas the dorsolateral margin of this foramen is formed by the orbitosphenoid in USNM 371299.

Marmosops bishopi is morphometrically similar to *M. chucha*, with which it exhibits overlapping variation in all same-sex comparisons of homologous measurement values. Apparently, the only diagnostically useful external character for these species is the coloration of the ventral pelage, which is almost entirely self-white in most specimens of *M. bishopi*, whereas the self-white midventral fur of *M. chucha* is often narrowed by lateral zones of gray-based fur. Craniodentally, these species can be distinguished by the dorsolateral margin of the ethmoid foramen (which is usually formed by the frontal bone in *M. bishopi*, but by the orbitosphenoid in *M. chucha*) and by the morphology of c1 (which has only a posterior accessory cusp in both sexes of *M. bishopi*, whereas female specimens of *M. chucha* have both anterior and posterior accessory cusps.

Marmosops bishopi is also morphometrically similar to *M. magdalenae*, with which it overlaps broadly in all external and craniodental measurements. However, these species differ—to about the same extent already described between *M. bishopi* and *M. chucha*—in ventral pelage color pattern: whereas most specimens of *M. bishopi* have entirely self-white ventral fur, all examined specimens of *M. magdalenae* have a narrower midventral zone of self-white fur flanked by broad lateral bands of gray-based hairs that sometimes extend onto the fore- and hind limbs. In addition, palatine fenestrae are consistently absent (or present as small, usually unilateral or asymmetrical perforations) in *M. bishopi*, whereas palatine foramina are large and well developed in *M. magdalenae*. Lastly, the talonid of m4 seems to be consistently tricuspid in *M. bishopi*, whereas the m4 talonid is usually bicuspid in *M. magdalenae*.

Remarks: *Marmosops bishopi* is a very widespread species that includes at least six cyto-

FIG. 21. Dorsal and ventral views of skulls of *Marmosops bishopi* (left, MUSM 23803) and *M. juninensis* (right, AMNH 230016). All views about ×3.

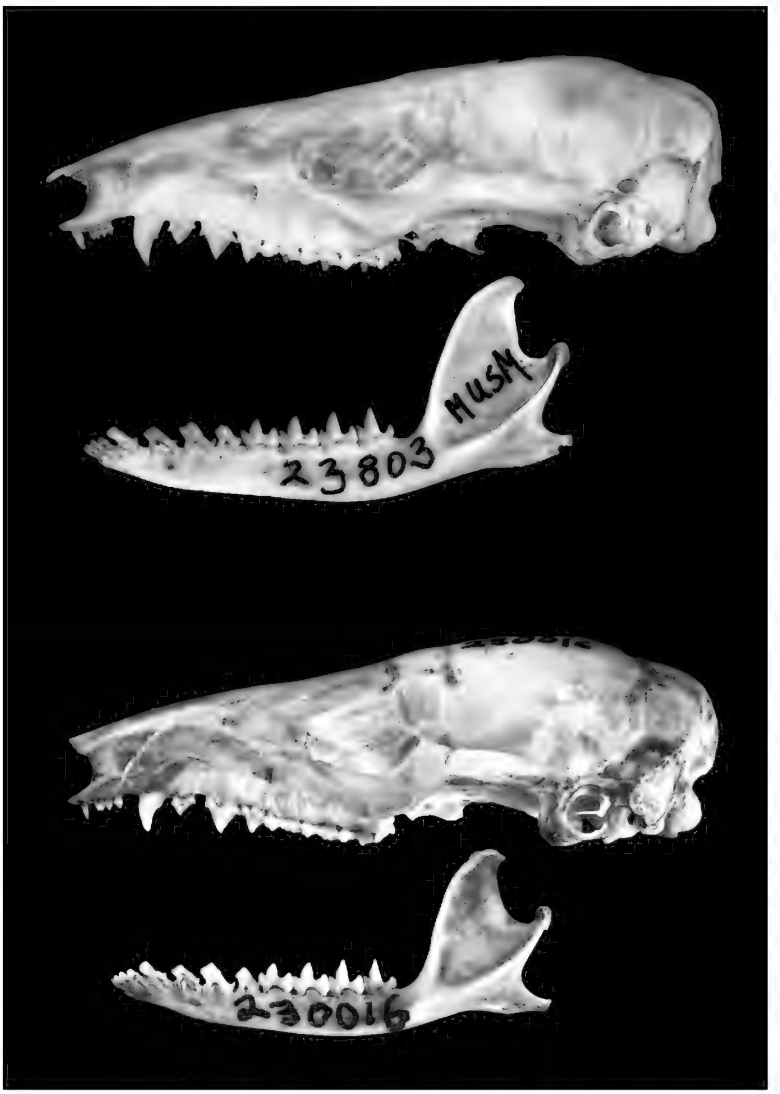

FIG. 22. Lateral views of skulls and mandibles of *Marmosops bishopi* (above, MUSM 23803) and *M. juninensis* (below, AMNH 230016). All views about ×3.

chrome-*b* haplogroups, which Díaz-Nieto et al. (2016a) distinguished by alphabetic labels (table 11). Genetic divergence among these haplogroups is impressively high, but we are unable to distinguish them morphologically. The most divergent haplogroup is "F," which differs from all of the others by >10% in uncorrected pairwise cytochrome-*b* sequence comparisons, whereas pairwise cytochrome-*b* distances among haplogroups A–E range from 3.5 to 5.3% (Díaz-Nieto et al., 2016a: supplementary information, table S3). We did not obtain any sequence data from the holotype, but the type locality is closest (geographically and ecologically) to the Cerrado site in eastern Bolivia (fig. 24: locality 5) where specimens with haplotype "E" were collected.

Specimens examined (N = 91): **Bolivia**—*Beni,* 1 km E La Emboscada (UMMZ 156014); *Cochabamba,* Serranía Mosetenes (CBF 7531); *La Paz,* Alto Río Madidi (USNM 579249), La Reserva

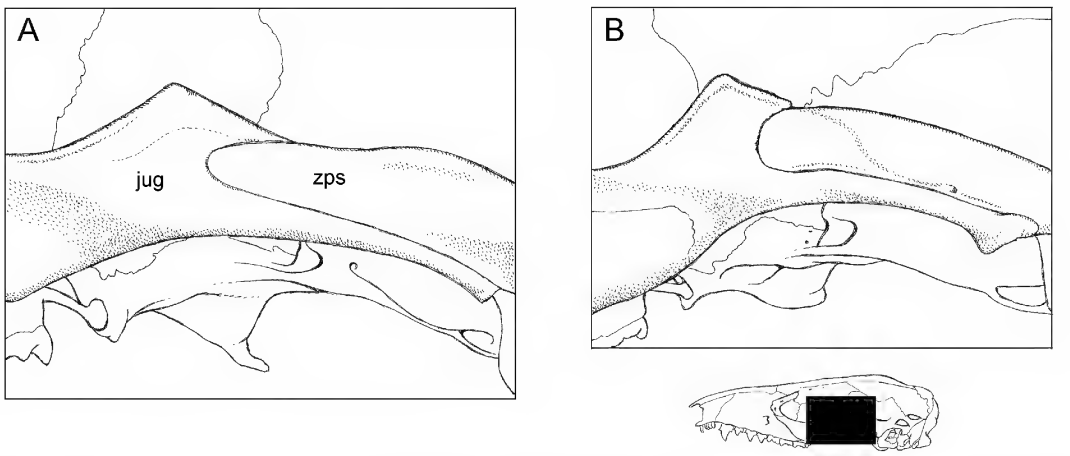

FIG. 23. Lateral view of zygomatic arch of *Marmosops bishopi* (**A,** MUSM 23803) and *M. juninensis* (**B,** AMNH 230016) illustrating species differences in the extent of dorsal overlap between the zygomatic process of the squamosal (**zps**) and the jugal (**jug**).

(AMNH 268938); *Santa Cruz,* El Refugio (USNM 584464, 584465), San Rafael de Amboró (MSB 55843). **Brazil**—*Amazonas,* Barro Vermelho (MVZ 190283), Vai-Quem-Quer (MVZ 190284); *Mato Grosso,* 264 km N Xavantina (USNM 393535 [holotype]). **Colombia**—*Amazonas*, Vereda Peña Roja (ICN 18338). **Ecuador**—*Morona Santiago*, Wisui (EPN 11947); *Napo*, Ituamani (EPN 127), Río Hollín (EPN 129); *Orellana*, Parque Nacional Yasuní (EPN 10706; QCAZ 8168, 8169, 11004); *Pastaza*, Arajuno (QCAZ 9954, 10074, 10308, 10606, 10608, 10661, 10758); *Sucumbíos*, Cantón Shushufindi (EPN 11686), El Reventador (QCAZ 316). **Peru**—*Amazonas*, Puerto Tunduza (MUSM 16237, 16240, 16241, 16243); *Cuzco*, Camisea (MUSM 14857), Cosñipata (FMNH 84251); *Huánuco,* Puerto Márquez (AMNH 67243); *Loreto,* Cocha Coconilla (MUSM 17691, 17723), Collpa Salvador (MUSM 17661), El Triunfo (MUSM 33445, 33487), Estación Biológica Allpahuayo (LACM 96113; TTU 98653, 98702, 98857, 98964, 99031, 99032, 100941, 101238, 101239, 101155, 101257), Jenaro Herrera (AMNH 276697, 276700, 276705, 276718, 276723; MUSM 15978–15981, 23799–23803), La Habana km 52 carretera Iquitos-Nauta (MUSM 33446), Nuevo San Juan (MUSM 13287), Quebrada Agua Negra (MUSM 24432), San Jacinto (KU 157969), San Lucas km 44 carretera Iquitos-Nauta (MUSM 33448, 33450, 33451), San Pedro (UF 30454), Teniente López (KU 157970, 157971), Trece de Febrero km 31.5 carretera Iquitos-Nauta (MUSM 33452); *Madre de Dios*, 2.75 km E Shintuya (FMNH 169802; MUSM 16803, 16804), 12 km E Puerto Maldonado (MVZ 168966), Blanquillo (MUSM 8396), Reserva Cuzco Amazónico (MUSM 6060, 6061), Río La Torre (MUSM 20087), S.N. Pampas del Heath (MUSM 11652); *San Martín*, Caserío El Diamante (FMNH 203328, 203509); *Ucayali*, Cerros de Canchaguaya (MUSM 17902, 17930, 17952).

Marmosops juninensis (Tate, 1931)

Figures 5B, 21, 22, 23B

Marmosa juninensis Tate, 1931: 13 (original description).

Marmosa parvidens juninensis: Pine, 1981: 64 (name combination).

Marmosops parvidens juninensis: Gardner, 1993: 20 (name combination).

Marmosops juninensis: Emmons, 1990: 22 (first use of current binomial).

Type material: The holotype (by original designation) consists of the skin and skull of a young adult female (AMNH 63864) collected by

TABLE 11

Cytochrome-*b* Haplogroups of *Marmosops bishopi*[a]

Haplogroup	*N*[b]	Distribution[c]	Biome(s)	Habitat(s)
A	7	eastern Peru & western Brazil	Amazonia & Andean foothills	lowland & premontane rain forest
B	1	northeastern Bolivia	Andean foothills	premontane rain forest
C	1	southeastern Colombia	Amazonia	lowland rain forest
D	2	northeastern Bolivia	Andean foothills	lowland & premontane rain forest
E	2	eastern Bolivia	Cerrado	semideciduous gallery forest
F	3	northeastern Peru	Amazonia	lowland rain forest

[a] After Díaz-Nieto et al. (2016a).
[b] Number of sequences.
[c] See Díaz-Nieto et al. (2016a: fig. 2) for mapped localities.

H. Watkins on 25 February 1929 at Utcuyacu (fig. 24: locality 68), between Tarma and Chanchamayo, in Junín department, Peru, at an altitude of 4800 feet (1463 m).

Distribution, habitats, and sympatry: Examined specimens suggest that *Marmosops juninensis* has a restricted distribution in premontane and montane rain forest on the eastern slopes of the Peruvian Andes in the departments of Junín and Pasco between 1387 and 2316 m above sea level. According to Peralta and Pacheco (2014), at the lower limit of its elevational range *M. juninensis* occurs sympatrically with *M. bishopi*, where at least two species of the nominotypical subgenus (*M. noctivagus* and a member of the *M. caucae* complex) could also be expected to occur.

Description: Body pelage reddish brown (near Prout's Brown) middorsally, indistinctly paler laterally, and about 7–9 mm long at midback; ventral pelage superficially whitish, but hairs extensively gray based on throat, chest, and abdomen (including the insides of the fore- and hind limbs), with or without a narrow, discontinuous midventral streak of self-white fur.[12] Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercles bladelike. Mammary formula unknown (no female specimens with visible teats were examined). Tail substantially longer than combined length of head and body (mean LT/HBL × 100 = 126%–137%); dorsal caudal surface dark (perhaps brownish in life), ventral surface indistinctly paler.

Nasals long (extending well behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; apex of zygomatic process of squamosal distinctively rounded anteriorly and not (or only slightly) overlapped dorsally by jugal. Palatine fenestrae consistently present, but sometimes irregular in size and shape. Dorsolateral margin of ethmoid foramen formed by the frontal.

Upper canine (C1) with only posterior accessory cusp in both sexes. Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp usually present but very small. First lower molar (m1) entoconid shorter than m2 paraconid; unworn m4 talonid with three distinct cusps.

Comparisons: Comparisons of *Marmosops juninensis* with *M. bishopi* are provided in the preceding account.

Marmosops juninensis seems to be about the same size as *M. ojastii* (table 8), but with the

[12] Voss et al. (2001: 48) described the ventral fur as "entirely gray-based," corresponding to the phenotype seen in AMNH specimens, but Peralta and Pacheco (2014) described and illustrated recently collected material with a midventral streak of self-white fur.

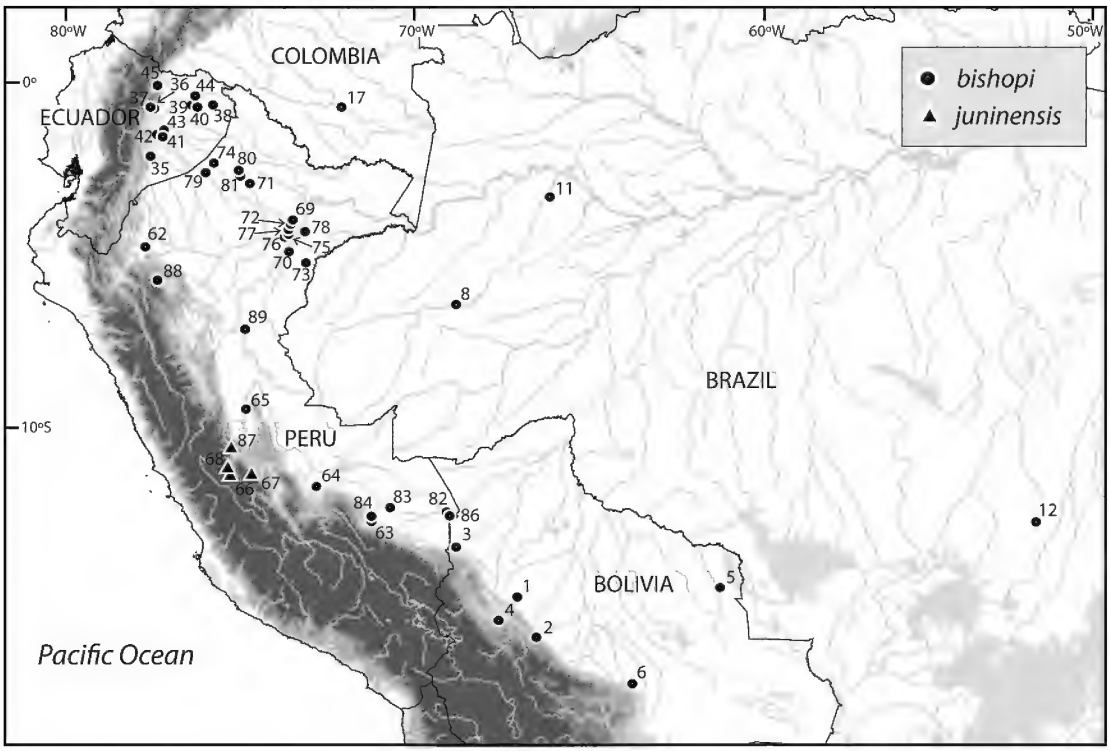

FIG. 24. Collecting localities of examined specimens of *Marmosops bishopi* and *M. juninensis*. Numbers are keyed to entries in the gazetteer (appendix 1). Progressively darker shading indicates higher elevations: pale gray ≥500 m, medium gray≥ 1000 m, dark gray ≥2000 m, darkest gray ≥3000 m.

small samples available for both species, morphometric inference is problematic. In side-by-side comparisons of skins these species are most readily distinguished by ventral pelage coloration: whereas the ventral pelage of *M. juninensis* is extensively gray based (with only a discontinuous midventral streak of self-white fur), the ventral pelage of *M. ojastii* is almost entirely self-white with no trace of gray-based hairs. *Marmosops juninensis* can also be unambiguously distinguished from *M. ojastii* by several craniodental characters including dorsal overlap between the squamosal and jugal (shallow or absent in *M. juninensis* versus extensive in *M. ojastii*), the dorsolateral margin of the ethmoid foramen (usually formed by the frontal in *M. juninensis* versus by the orbitosphenoid in *M. ojastii*), palatine fenestrae (consistently present in *M. juninensis* versus absent in *M. ojastii*), and a lingual accessory cusp on c1 (present in *M. juninensis* but absent in M. *ojastii*).

Insofar as can be judged from our small samples, *Marmosops juninensis* and *M. chucha* are about the same size. Skins of these species are distinguishable by ventral pelage coloration, which is extensively gray based in *M. juninensis* (notably on the throat and inside surfaces of the fore- and hind limbs) but broadly self-white in *M. chucha* (in which the throat is always self-white and the inside surfaces of the limbs usually have some self-white markings). In qualitative cranial comparisons, these species can be readily distinguished based on squamosal-jugal overlap (the jugal only slightly overlaps the zygomatic process of the squamosal in *M. juninensis*, whereas dorsal overlap between the jugal and squamosal bone is extensive in *M. chucha*), palatine fenestration (palatine fenestrae are consis-

tently present and large in *M. juninensis* whereas palatine fenestrae are minute or absent in *M. chucha*), and the lingual accessory cusp of c1 (usually present in *M. juninensis* versus usually absent in *M. chucha*).

Marmosops juninensis is likewise similar in size to *M. magdalenae*, from which it cannot confidently be distinguished based on measurement data alone. However, these species are distinguishable by ventral pelage coloration (extensively gray based in *M. juninensis* versus extensively self-white in *M. magdalenae*), dorsal overlap between the jugal and squamosal zygomatic process (shallow or absent in *M. juninensis* versus extensive in *M. magdalenae*), the lingual accessory cusp on c1 (usually present in *M. juninensis* versus usually absent in *M. magdalenae*), and the number of m4 talonid cusps (three in *M. juninensis* versus two in *M. magdalenae*).

Remarks: The Pasco specimen (LSU 25902) is a juvenile male, but it is a good match in pelage and dental traits with other material referred to this species. In particular, the ventral fur of LSU 25902 is entirely gray based, C1 has a distinct posterior accessory cusp, and the combined length of M1–M2 is 3.5 mm (versus 3.4–3.6 mm in AMNH specimens, including the holotype).

Specimens examined (N = 7): **Peru**—*Junín,* San Antonio (MUSM 40616, 40617), 22 mi E Tarma (AMNH 230014–230016), Utcuyacu (AMNH 63864); *Pasco,* Santa Cruz (LSU 25902).

Marmosops ojastii García et al., 2014

Figures 25–27

Marmosops ojastii García et al., 2014: 704 (original description).

Type material: The holotype (by original designation) consists of a fluid preserved body and skull of an adult male (EBRG 27474) said to have been collected by Frank Steines on 27 February 1996 at Pico Guacamaya (fig. 28: locality A), Parque Nacional Henri Pittier, Cordillera de la Costa, Aragua, Venezuela. Additionally, García et al. (2014: 705) designated one paratype (EBRG 29540), but excluded four other examined specimens (EBRG 27475, 27476, 29566, 29587) from the type series.

Distribution, habitats, and sympatry: *Marmosops ojastii* occurs in the Cordillera de la Costa and adjacent lowlands of northern Venezuela and in the Cordillera de Mérida of western Venezuela (fig. 28) from near sea level to at least 1850 m. Habitats within this elevational range include lowland rain forest (e.g., near Urama; Handley, 1976: 84) and premontane rainforest (e.g., at Pico Guacamayo; García et al., 2014: 713, fig. 7). This species apparently occurs sympatrically with *M. carri* at Rancho Grande (appendix 1: locality 103) and may do so throughout its geographic range.

Description: Dorsal body pelage pale reddish brown and about 8–10 mm long at midback;[13] ventral pelage self-white from chin to groin (including the inside surfaces of the fore- and hind limbs), without lateral zones of gray-based hairs. Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercle bladelike, not spoon shaped. Mammary formula unknown (no adult female specimens examined by us or by García et al., 2014). Tail considerably longer than combined length of head and body (mean LT/HBL × 100 = 143%) and indistinctly bicolored.

Nasals apparently not very long (not extending posteriorly much behind the lacrimals) and wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; zygomatic process of the squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae absent. Dorsolateral margin of ethmoid foramen formed by the orbitosphenoid.

Upper canines short and apparently not sexually dimorphic; males and females with posterior

[13] Near Buffy Brown middorsally and somewhat paler laterally in USNM 371299, "marrón rojizo" in specimens examined by García et al. (2014: 707). The dorsal fur is a little shorter in USNM 371299 (collected near sea level) than in the material measured by García et al. (2014) from higher elevations.

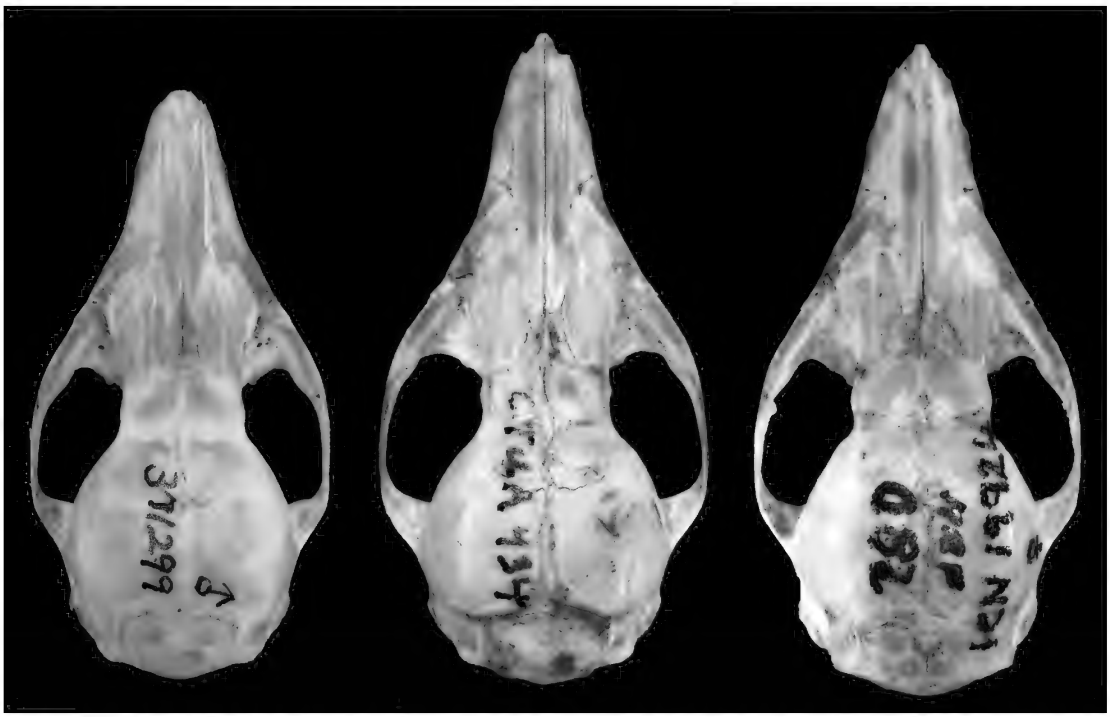

FIG. 25. Dorsal views of skulls of *Marmosops ojastii* (left, USNM 371299), *M. chucha* (center, CTUA 434), and *M. magdalenae* (right, ICN 19924). All views about ×3.

accessory cusp only.[14] Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent. Entoconid of m1 shorter than adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

Comparisons: Comparisons of *Marmosops ojastii* with *M. bishopi* and *M. juninensis* have already been provided in the preceding species accounts (above).

Marmosops ojastii appears to be smaller, on average, than *M. chucha* (table 8). In fact, males of these allopatric species exhibit nonoverlapping variation in several external and craniodental dimensions (e.g., HBL, NB, LIB, PL, PB, MTR, LM), although the diagnostic value of these data is compromised by small sample sizes. The single skin of *M. ojastii* available for side-by-side comparisons with skins of *M. chucha* is conspicuously paler than any of the latter species, and it has more extensively self-white underparts than most skins of *M. chucha* (which often have lateral zones of gray-based ventral fur). Additionally, *M. ojastii* appears to have a relatively longer tail (about 140% of HBL) by comparison with *M. chucha* (about 130% of HBL). Skulls of the two species are qualitatively similar, but (in addition to the aforementioned size difference) the nasals of *M. ojastii* are visibly narrower in proportion to interorbital breadth than are those of *M. chucha* (NB/LIB = ca. 0.57 versus 0.70, respectively, for males). Whereas males and females of *M. ojastii* have only a posterior accessory cusp on C1, most female specimens of *M. chucha* have both anterior and posterior C1 accessory cusps.

Marmosops ojastii appears to differ from *M. magdalenae* in many of the same traits that

[14] We have not examined any female specimens, but García et al. (2014) described two juvenile females with a posterior accessory cusp on C1.

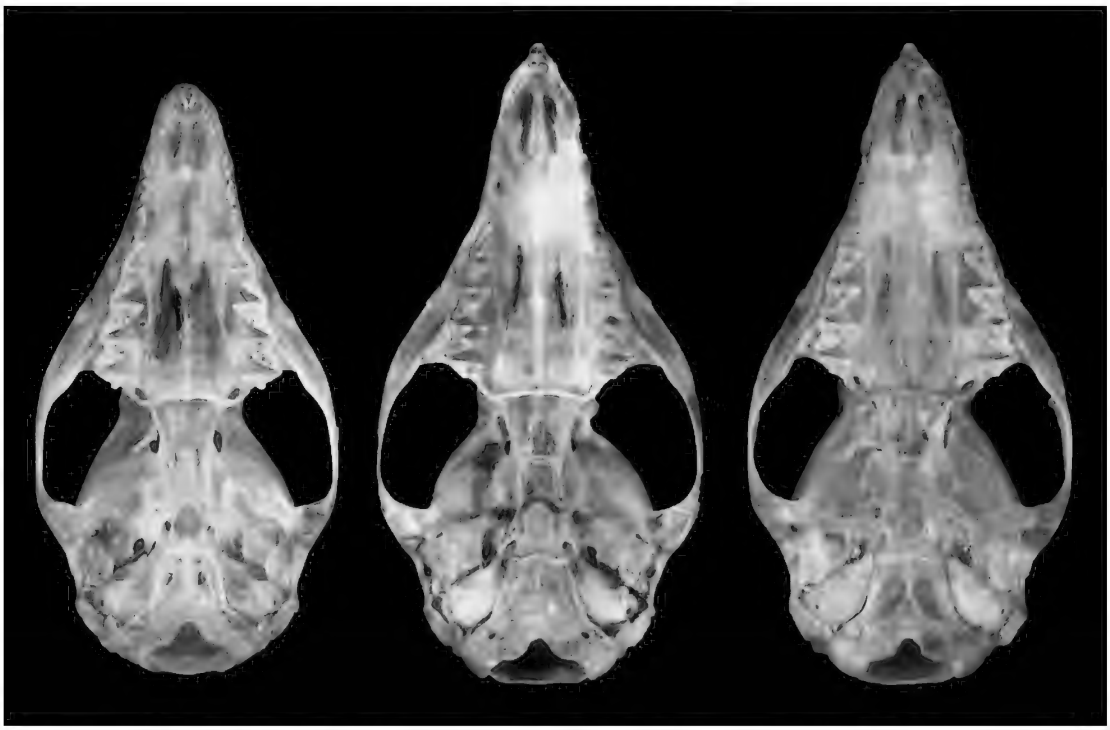

FIG. 26. Ventral views of skulls of *Marmosops ojastii* (left, USNM 371299), *M. chucha* (center, CTUA 434), and *M. magdalenae* (right, ICN 19924). All views about ×3.

apparently distinguish it from *M. chucha*, including smaller size, paler dorsal pelage, more extensively self-white ventral pelage, longer tail (relative to head-and-body), and narrower nasals (relative to interorbital breadth). Additionally, palatine fenestrae are absent in both intact adult skulls of *M. ojastii* (fig. 26; García et al., 2014: fig. 2B), whereas these openings are consistently present in examined specimens of *M. magdalenae* (figs. 5C, 26). Other possibly diagnostic characters include the dorsolateral margin of the ethmoid foramen (formed by the orbitosphenoid in USNM 371299, but by the frontal in examined specimens of *M. magdalenae*), and the number of m4 talonid cusps (three in USNM 371299, usually two in *M. magdalenae*).

Remarks: The single specimen of *Marmosops ojastii* that we examined (USNM 371299) was not part of García et al.'s (2014) type material, but it agrees with their morphological description in all important respects, its measurements correspond closely to their measurements of the holotype skull and paratype skin, and it was collected within the geographic range of their material (fig. 28). Those authors did not analyze any genetic data, so it is relevant to note that the cytochrome-*b* sequence we obtained from USNM 371299 is highly divergent (by 9%–15% in average pairwise uncorrected comparisons; Díaz-Nieto et al., 2016a: supplementary information, table S3) from those of previously described taxa in the subgenus *Sciophanes* and tends to support the conclusion that *M. ojastii* is a valid species. This specimen was previously identified as *M. parvidens* by Pine (1981) and Voss et al. (2001: 48–49), although the latter authors remarked several of the traits that we now recognize as diagnosing the Bishopi Group (e.g., its bladelike carpal tubercle and lack of an anterior C1 accessory cusp).[15]

[15] According to García et al. (2014: 715), USNM 371299 is a juvenile, but in fact it is a young adult.

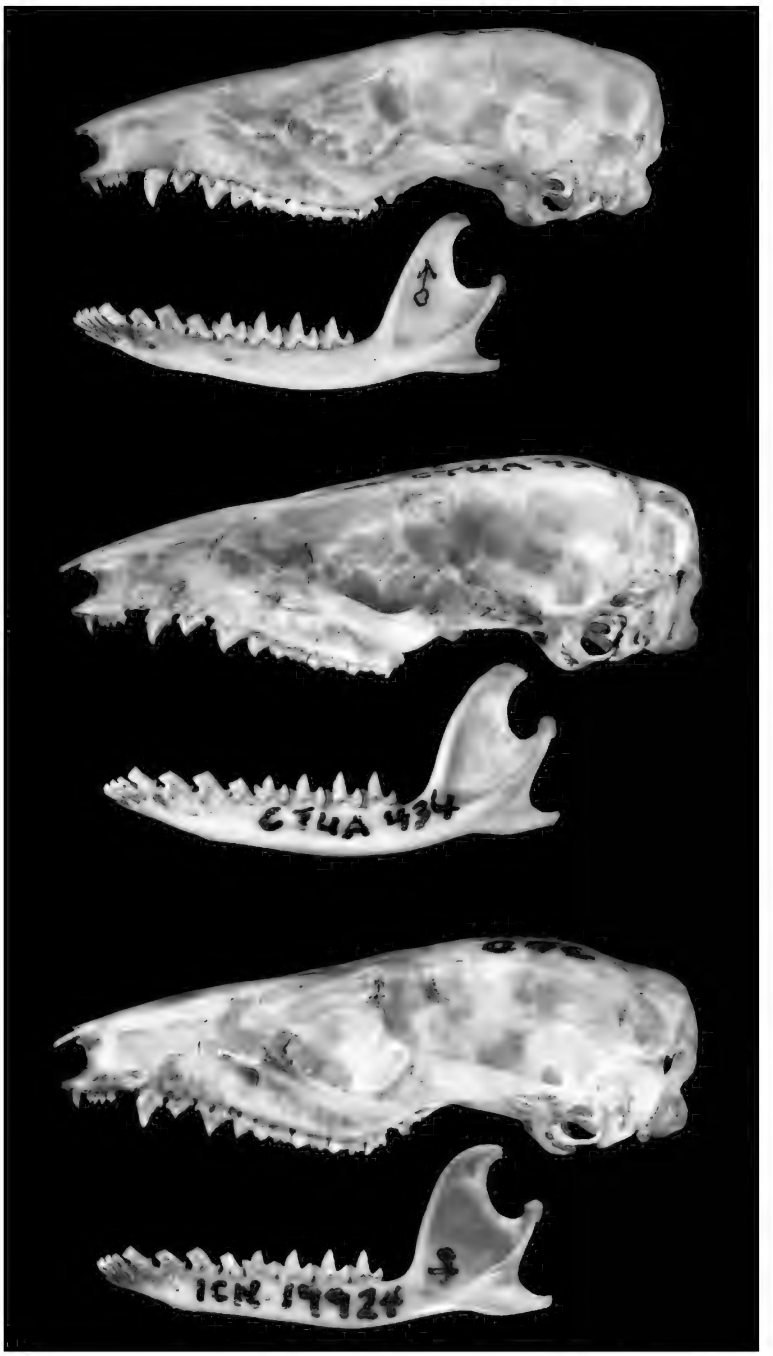

FIG. 27. Lateral views of skulls of *Marmosops ojastii* (above, USNM 371299), *M. chucha* (center, CTUA 434), and *M. magdalenae* (below, ICN 19924). All views about ×3.

A single specimen from the Maracaibo Basin of western Venezuela (UMMZ 53222), a fluid-preserved adult male with an extracted skull, might also represent this species. Like other members of the Bishopi Group, it has bladelike carpal tubercles, and the anterior cingulum of M3 is narrowly continuous. Like *M. ojastii*, it has completely self-white underparts, lacks palatine fenestrae, and has narrow nasals relative to interorbital breadth (NB/LIB = 0.54). Unlike *M. ojastii*, however, the upper canine of UMMZ 53222 has well-developed anterior and posterior accessory cusps. Unfortunately, we were unable to amplify DNA from this old specimen (collected in 1914; see appendix 1: locality 118), and we are unaware of any additional material from the Maracaibo lowlands, which are now extensively deforested.

In their phylogenetic analyses of *Marmosops*, Díaz-Nieto et al. (2016a: figs. 4, 5) were not able to convincingly resolve the position of *M. ojastii*, which was either recovered as the sister taxon of *M. chucha* + *M. magdalenae* (using cytochrome-*b* sequences only) or as the sister species of *M. bishopi* (using sequences from cytochrome-*b* and the Breast Cancer Activating 1 nuclear gene).

Specimens examined (N = 1): **Venezuela—***Carabobo/Falcón/Yaracuy,* 19 km NW Urama (USNM 371299).

Marmosops chucha, new species

Figures 25–27

Holotype: CTUA 434 (original number CACE004), consisting of the skin, skull, fluid-preserved carcass, and associated tissues of an adult female collected by Camilo A. Calderón-Acevedo on 15 July 2010 at Hacienda Vegas de La Clara (fig. 28: locality 18), municipio Gómez Plata, Antioquia, Colombia.

Distribution, habitats, and sympatry: Examined specimens of *Marmosops chucha* are from west of the Río Magdalena in northern Colombia between 130 m and 1400 m; known collection localities are in the foothills of the Serranía de Abibe (the northwestern terminus of the Cordillera Occidental), the northeastern part of the Cordillera Central, and the interandean valley of the Río Porce (fig. 28). Recorded capture habitats include premontane rain forest (Sánchez-Giraldo and Díaz-Nieto, 2015), premontane moist forest (Estrada-Pareja et al., 2007), and lowland rain forest (Castaño and Corrales, 2010), all of which now occur as fragments within an anthropogenic matrix of pastures and agricultural fields. At the upper limit of its known elevational range, *M. chucha* occurs sympatrically with *M. handleyi* (e.g., near Valdivia [appendix 1: locality 24]; see Díaz-N. et al., 2011).

Description: Body pelage brownish (near Prout's Brown in darker specimens, closer to Dresden Brown in others) middorsally, indistinctly paler laterally, and about 7–10 mm long at midback; ventral pelage continuously self-white from chin to groin (usually including the insides of the fore- and hind limbs), but self-white fur narrowed by lateral zones of gray-based abdominal fur (tipped with brown) in some specimens.[16] Manus covered dorsally with uniformly pale hairs (the metacarpals not contrasting sharply in color with the digits); lateral carpal tubercle bladelike, not spoon shaped. Mammary formula 4–1–4 = 9 in all examined females with visible teats. Tail substantially longer than combined length of head and body (mean LT/HBL × 100 = 130%), usually indistinctly bicolored and sometimes indistinctly paler distally than basally.

Nasals not very long (usually not extending posteriorly behind the lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; zygomatic process of squamosal broadly overlapped dorsally by the jugal. Palatine fenestrae absent or minute. Dorsolateral margin of ethmoid foramen formed by the orbitosphenoid.

[16] This might be a sexually dimorphic trait. The midventral zone of self-white fur—measured across the sternum—seems to be wider in females (17–20 mm, N = 3) and narrower in males (7–12 mm, N = 5).

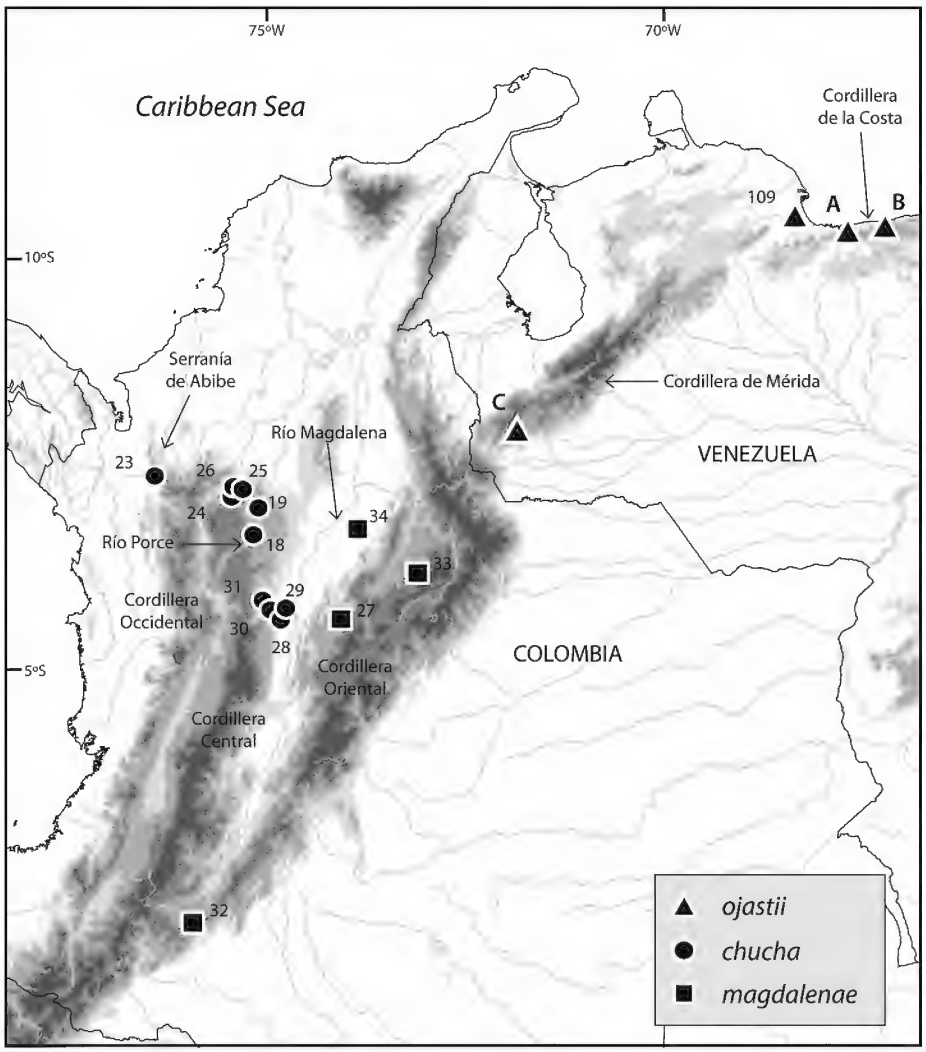

FIG. 28. Collecting localities of *Marmosops ojastii*, *M. chucha*, and *M. magdalenae*. Numbers are keyed to entries in the gazetteer for material examined by us; letters indicate collection localities of unexamined material of *M. ojastii* reported by García et al. (2014): **A,** Pico Guacamaya, Parque Nacional Henri Pittier, Aragua, Venezuela (10°21′ N, 67°40′ W); **B,** Sector Buenos Aires, Monumento Nacional Pico Codazzi, Aragua, Venezuela (10°25′N, 67°21′W); **C,** Campamento La Trampita, Uribante-Caparo, Táchira, Venezuela (7°50′ N, 71°57′W). Progressively darker shading indicates higher elevations: pale gray ≥500 m, medium gray ≥1000 m, dark gray ≥2000 m, darkest gray ≥3000 m.

Upper canines short in both sexes but apparently sexually dimorphic: males usually with only posterior accessory cusp and females usually with both anterior and posterior accessory cusps (MHNUC 986, a male with both anterior and posterior accessory cusps, and FMNH 69822, a female with just a posterior accessory cusp, are exceptions). Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent in most examined material (but dis-

tinctly present in FMNH 70925). Entoconid of m1 shorter than adjacent m2 paraconid; unworn m4 talonid with three distinct cusps.

Comparisons: Comparisons of *Marmosops chucha* with *M. bishopi*, *M. juninensis*, and *M. ojastii* have already been provided in the accounts for those species (above).

Marmosops chucha and *M. magdalenae* are similar in most qualitative and morphometric traits, but palatine fenestrae are consistently absent or indistinct in *M. chucha*, whereas these openings are consistently large in *M. magdalenae*. Additionally, the dorsolateral margin of the ethmoid foramen is usually formed by the orbitosphenoid in *M. chucha* whereas the dorsolateral margin of this foramen is usually formed by the frontal in *M. magdalenae*. Lastly, there are apparent taxonomic differences in the presence of C1 accessory cusps: in *M. chucha* most males have only posterior accessory cusps and most females have both anterior and posterior cusps, whereas in *M. magdalenae* both sexes have only posterior accessory cusps.

Etymology: From *chucha*, a colloquial term for "opossum" in Colombian Spanish (Comisión de Lingüística de la Academia Colombiana, 2012), here treated as a noun in apposition.

Remarks: The known geographic ranges of *Marmosops chucha* and *M. magdalenae* are separated by the Río Magdalena, an important geographic barrier (Chapman, 1917; Gutiérrez-Pinto et al., 2012), and they differ from one another by about 5.9% in average uncorrected pairwise comparisons of partial cytochrome-*b* sequences. Although additional phenotypic and genetic evidence that these are fully differentiated species would be welcome, the results at hand seem sufficient to justify their recognition as such in the context of this revision.

The material that we refer to *Marmosops chucha* was previously identified as *Marmosa parvidens* by Pine (1981), as *Marmosops parvidens* by Díaz-N. et al. (2011), and as *Marmosops* "West Magdalena" by Díaz-Nieto et al. (2016a).

Specimens examined ($N = 10$): **Colombia**—*Antioquia*, Amalfi (CTUA 428), Gómez Plata (CTUA 434), Valdivia (FMNH 69822, 69825, 69826), Villa Arteaga (FMNH 69837); *Caldas*, Norcasia (MNHUC 750, 986), Samaná (FMNH 70925; MNHUC uncataloged DCV69).

Marmosops magdalenae, new species

Figures 5C, 6B, 25–27

Holotype: ICN 19924 (original number MRP82), consisting of the skin and skull of an adult female collected by Miguel E. Rodríguez-Posada on 18 July 2002 at Bosque de Roble Cerca de Torre, Reserva Biológica Cachalú (fig. 28: locality 33), vereda Rionegro, municipio Encino, Santander, Colombia.

Distribution and sympatry: Examined specimens of *Marmosops magdalenae* are from east of the Río Magdalena in northern Colombia, where it has been collected between 104 m and 1940 m above sea level (fig. 28). Capture habitats include lowland rain forest along the right bank of the Río Magdalena (e.g., at Corregimiento Campo Capote [fig. 28: locality 34]) and lower montane moist forest on the western slope of the Cordillera Oriental (e.g., at Reserva Biológica Cachalú [fig. 28: locality 33]; Otálora-Ardila, 2003; Ávila et al., 2010). This species is not known to occur sympatrically with any other congener, but at the upper limit of its elevational range it might cooccur with *M. caucae*, a member of the nominotypical subgenus that is widespread in Andean cloud forests (Díaz-Nieto et al., 2016a).

Description: Body pelage fuscous to reddish brown (near Dresden Brown) middorsally, indistinctly paler laterally, and about 9 mm long at midback (based on FMNH 70926); ventral pelage self-white from chin to groin (including the inside surface of the forelimbs and sometimes also the hind limbs), but midventral band of self-white fur narrowed by lateral zones of gray-based abdominal hairs (sometimes with brownish tips) on abdomen. Manus covered dorsally with uniformly pale fur, without pigmental contrast between the metacarpal and digital pelage; lateral carpal tuber-

cles bladelike in all examined adult males. Mammary formula unknown.[17] Tail longer than combined length of head and body (mean LT/HBL × 100 = 125%–130%), indistinctly bicolored, and somewhat paler distally than proximally (but not distinctly particolored).

Nasals not very long (usually not extending posteriorly behind lacrimals) and much wider posteriorly than anteriorly (laterally expanded at the maxillary-frontal suture). Lacrimal foramina concealed from lateral view inside anterior orbital margin; zygomatic process of squamosal broadly overlapped dorsally by jugal. Palatine fenestrae consistently present and large. Dorsolateral margin of ethmoid foramen usually formed by the frontal.

Upper canines short, with posterior accessory cusps in both sexes (anterior accessory cusps consistently absent in all examined material). Upper third molar (M3) anterolabial cingulum narrowly continuous with preprotocrista (anterior cingulum complete). Lower canine (c1) premolariform (procumbent, with posterior accessory cusp) and small, subequal in height to p1; c1 anterolingual accessory cusp absent or indistinct. Entoconid of m1 shorter than adjacent m2 paraconid; unworn m4 talonid usually with only two distinct cusps.

Comparisons: Comparisons between *Marmosops magdalenae* and other species of the Bishopi Group have already been provided in the preceding accounts.

Etymology: For the Río Magdalena, economically and culturally the most important river of Colombia, and a well-known dispersal barrier for the terrestrial vertebrate fauna of northwestern South America (Chapman, 1917; Gutiérrez-Pinto et al., 2012).

Remarks: The material that we refer to *Marmosops magdalenae* was previously identified in the literature as *Marmosa parvidens* by Pine (1981), as *Marmosops parvidens* by Díaz-N. et al. (2011), and as *Marmosops* "East Magdalena" by Díaz-Nieto et al. (2016a).

Specimens examined (N = 3): **Colombia**—*Boyacá,* Muzo (FMNH 70926); *Huila*, near San Adolfo (FMNH 70927, 70928); *Santander*, Encino (ICN 19924), Puerto Parra (ICN 18788).

DISCUSSION

Specimens of the subgenus *Sciophanes* are not common in museum collections. Although we examined all the material that we were able to locate in North American, Colombian, and Ecuadorean museums, the total available for this study of 12 species amounted to fewer than 300 specimens. By contrast, Rossi et al. (2010) were able to examine almost 1500 specimens for their revision of just seven species of *Marmosa*. This difference in specimen availability perhaps reflects the difficulty of trapping very small marsupials like *Sciophanes* with commercially available equipment. Pitfall trapping appears to be a more effective collecting method (Voss et al., 2001: table 48), but pitfalls have only recently come into routine use for Neotropical rainforest mammal inventory work (Umetsu et al., 2006; Ribeiro-Júnior et al., 2011). As pitfall trapping continues to gain in popularity, we predict a corresponding increase in numbers of fresh specimens of *Sciophanes*, which should provide abundant material for evaluating the taxonomic conclusions of our study.

Even a cursory examination of the maps in this report suggests where new discoveries are likely to be made. We have not seen any material of *Sciophanes* from vast Amazonian landscapes, including those drained by such major rivers as the Rio Negro, the Tapajos, the Madeira, and the upper Xingu. No specimens are known from the eastern slopes of the Colombian Andes, nor from the Chocó lowlands of western Colombia. Based on the distribution of other small didelphids that often cooccur with *Sciophanes*, it seems likely that the subgenus does occupy many regions

[17] The skin tag of ICN 19924 mentions the presence of "6 mamas," but no mammary formula was provided. We inspected the skin of this specimen and found 6 teats in the arrangement 3–1–2. Because no species of *Marmosops* is known to have unpaired lateral mammae it seems probable that additional mammae are normally present in this species.

from which specimens are currently unknown. Therefore, we confidently predict that future collecting will result either in significant geographic-range extensions of currently recognized taxa, or in the discovery of new species. In effect, this report is no more than a preliminary assessment of the species-level diversity of *Sciophanes* based on the material now at hand.

Future research might also profitably focus on assessing the genetic independence of several mtDNA haplogroups that we are currently unable to distinguish by phenotypic criteria. In particular, coalescent analyses of nuclear markers could help determine whether any of the several haplogroups of *M. bishopi* (table 11) are cryptic species. On the other hand, morphological analyses would be welcome in any future attempt to evaluate the taxonomic status of populations with *M. pinheiroi*-like mtDNA sequences from savanna landscapes in Maranhão (Nascimento et al., 2015), and larger sample sizes would certainly be helpful for testing the statistical significance of morphometric differences inferred from small numbers of specimens in this study.

There is still much to learn.

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APPENDIX 1

Gazetteer

This gazetteer includes all localities from which we personally examined specimens of *Marmosops* (*Sciophanes*) for this report. Numbers correspond to specimen records plotted on maps in the text. Italicized place names are those of the largest political divisions (state, department, province, etc.) within each country. Boldface identifies collection localities as they appear in the text of this report. For each entry we provide geographic coordinates and elevation above sea level (in parentheses if recorded by the collector, otherwise in square brackets), name(s) of the species collected there, name(s) of the collector(s), and date(s) of collection. Units of distance (kilometers [km] or miles [mi]) are those recorded by the collector(s), as are units of elevation (meters [m] or feet [ft] above sea level).

BOLIVIA

1. *Beni,* **1 km E La Emboscada** [= La Embocada at 15°03′S, 66°58′W, 600 m; Anderson, 1997], Estancia La Cabaña: *Marmosops bishopi* (G.K. Creighton, 13 November 1979).
2. *Cochabamba,* **Serranía Mosetenes** (16°14′S, 66°25′W, 1300 m): *Marmosops bishopi* (E. Yensen, 3 September 2003).
3. *La Paz,* Iturraldi, **Alto Río Madidi** [13°35′S, 68°46′W, 270 m; Anderson, 1997]: *Marmosops bishopi* (L.H. Emmons, 27 May 1990).
4. *La Paz,* **La Reserva** (15°44′S, 67°31′W, 840 m): *Marmosops bishopi* (T. Tiurina, 22 July 1992).
5. *Santa Cruz,* **El Refugio** (14°46′S, 61°02′W, ca. 200 m): *Marmosops bishopi* (L.H. Emmons, 6–15 November 1998).
6. *Santa Cruz,* **San Rafael de Amboró** (17°36′S, 63°36′W, 400 m): *Marmosops bishopi* (B.R. Riddle, 31 July 1985).

BRAZIL

7. *Amapá,* **Serra do Navio** (including sublocalities "Rio Amapari" and "Km 190 EFA") [ca. 0°59′N, 52°03′W, 100 m; Paynter and Traylor, 1991]: *Marmosops pinheiroi* (F. de P. Pinheiro, 16 September 1969–8 May 1970).
8. *Amazonas,* **Barro Vermelho**, left bank Rio Juruá (6°28′S, 68°46′W): *Marmosops bishopi* (J.L. Patton, 25 October 1991).
9. *Amazonas,* Faro, **Boca Rio Paratucu** [= Rio Piratucu, mouth at 1°59′N, 56°58′W; Paynter and Traylor, 1991]: *Marmosops parvidens* (A.M. Olalla, 21 December 1930).
10. *Amazonas,* MCSE Reserves, **80 km N Manaus** (2°25′S, 59°50′W): *Marmosops parvidens* (J.R. Malcolm, 7 October 1983–4 September 1985).
11. *Amazonas,* **Vai-Quem-Quer**, right bank Rio Juruá [3°19′S, 66°01′W; Patton et al., 2000]: *Marmosops bishopi* (J.R. Malcolm, 14 May 1992).
12. *Mato Grosso,* **264 km N (by road) Xavantina**, Serra do Roncador [12°51′S, 51°46′W, 1750 ft; Pine, 1981]: *Marmosops bishopi* (R.H. Pine, 5 July 1968).
13. *Pará,* **52 km SSW Altamira** (3°39′S, 52°22′W), east bank Rio Xingu: *Marmosops pinheiroi* (M.D. Carleton, 15 September 1986).
14. *Pará,* **Belém** [1°27′S, 48°29′W; Paynter and Traylor, 1991]: *Marmosops pinheiroi* (collector unknown, 25 May 1970).
15. *Pará,* Rio Tocantins, **Ilha do Taiuna** [ca. 2°15′S, 49°30′W]: *Marmosa parvidens* (A.M. Olalla, 2 November 1931).
16. *Pará,* **Utinga** [near Belém, ca. 1°27′S, 48°29′W (see above); including sublocalities "Agua Preta," "Nova Area Experimental," and "Trapping Area 1"]: *Marmosops pinheiroi* (R.H. Pine, 10–14 June 1968; A.P. Souza, 18 February–25 June 1965 and 3 August 1967).

COLOMBIA

17. *Amazonas*, Leticia, **Vereda Peña Roja** [0°41′S, 72°08′W, 300m; Díaz-N., 2012]: *Marmosops bishopi* (P. Rivas P., 31 March 2004).
18. *Antioquia*, Gómez Plata, **Hacienda Vegas de la Clara** (6°35′22″N, 75°11′49″W, 1120 m): *Marmosops chucha* (C.A. Calderón-Acevedo, 16 July 2014).
19. *Antioquia,* Municipio Amalfi, **Porce Tres** [6°56′N, 75°08′W, 660 m; Google Earth at the crest of the wall of the dam]: *Marmosops chucha* (M. Bernal, 6 September 2004).
20. *Antioquia,* Municipio Amalfi, Vereda Guayabito, **Finca Costa Rica**, Bosque Caracolí (6°52′N, 75°06′W, 1840 m): *Marmosops handleyi* (C. Sánchez-Giraldo, J.F. Díaz-Nieto, D. Marín-C., November 2004–February 2008).
21. *Antioquia,* Municipio Yarumal, Corregimiento El Cedro, Vereda Corcovado, **Finca El Bosque**, Bosque San Andrés (7°04′N, 75°25′W, 1760 m): *Marmosops handleyi* (C. Sánchez-Giraldo, J.F. Díaz-Nieto, 1–2 October 2005).
22. *Antioquia,* Municipio Yarumal, Corregimiento El Cedro, Vereda El Rosario, sitio Alto de Ventanas, **Finca Villa Nueva** (7°05′N, 75°27′W, 1950 m):

Marmosops handleyi (C. Sánchez-Giraldo, J.F. Díaz-Nieto, 9–11 January 2006).

23. *Antioquia,* Urabá, **Villa Arteaga** ([7°20′N, 76°26′W; Hershkovitz, 1977], 130 m): *Marmosops chucha* (P. Hershkovitz, 28 January 1950).
24. *Antioquia,* Valdivia, **9 km S Valdivia** ([7°06′N, 75°28′W; Anderson, 1999], 1400 m): *Marmosops handleyi* (P. Hershkovitz, 16–18 June 1950), *M. chucha* (P. Hershkovitz, 17 June 1950).
25. *Antioquia,* Valdivia, **La Cabaña** [ca. 7°10′N, 75°25′W; based on P. Hershkovitz field notes]: *Marmosops chucha* (P. Hershkovitz, 22 June 1950).
26. *Antioquia,* Valdivia, **Quebrada Valdivia** ([7°10′N, 75°26′W; Anderson, 1999], 900 m): *Marmosops chucha* (P. Hershkovitz, 30 June 1950).
27. *Boyacá,* **Muzo** [5°32′N, 74°06′W, 1300 m; Paynter, 1997]: *Marmosops magdalenae* (P. Hershkovitz, 15 August 1952).
28. *Caldas*, Norcasia, **Vereda Montebello**, entre las fincas El Horizonte y La Albania, quebrada La Albania (5°34′48″N, 74°55′46″W, 817 m): *Marmosops chucha* (J.H. Castaño, 6 April 2014).
29. *Caldas*, Norcasia, Vereda San Roque, **Reserva Natural Río Manso** (05°40′08″N, 74°47′17″W, 200 m): *Marmosops chucha* (J.H. Castaño, 26 November 2009).
30. *Caldas*, Samaná, Corregimiento San Diego, **Vereda La Sonrisa** [5°37′N, 74°57′W, 900 m; Google Earth at "Vereda La Sonrisa"], Finca La Sonrisa: *Marmosops chucha* (D.C. Villanueva-C., 1 April 2014).
31. *Caldas,* Samaná, **Río Honda** ([5°42′N, 75°01′W; Hershkovitz, 1997], 1200 m): *Marmosops chucha* (P. Hershkovitz, 26 February 1951).
32. *Huila,* Acevedo, Río Aguas Claras, **near San Adolfo** ([ca. 1°37′N, 75°59′W; Paynter, 1997], 1400–1700 m): *Marmosops magdalenae.* (P. Hershkovitz, 21–28 June 1951).
33. *Santander*, Encino, Vereda Rionegro, **Reserva Biológica Cachalú**, Bosque de Roble Cerca de Torre (6°6′50″N, 73°8′10″W, 1940 m): *Marmosops magdalenae* (M.E. Rodríguez-Posada, 18 July 2002).
34. *Santander*, Puerto Parra, Vereda India Baja, **Corregimiento Campo Capote** [6°40′N, 73°53′W, ca. 104 m; Instituto Geográfico Agustín Codazzi, 2015]: *Marmosops magdalenae* (Y. Muñoz-Saba, 11 March 2012).

ECUADOR

35. *Morona Santiago*, Parroquia Macuma, **Wisui** [2°07′N, 77°44′W, 650 m; Arguero et al., 2012]: *Marmosops bishopi* (A. Arguero, and F. Sánchez, 21 July 2013).
36. *Napo*, **Huamaní** [0°43′S, 77°37′W, 1250 m; Gardner, 2008]: *Marmosops bishopi* (R. Mena, 27 August 1992).
37. *Napo*, parroquia Cotundo, **R**ío Hollín [0°41′S, 77°44′W, 1105 m; Moreno and Albuja, 2005]: *Marmosops bishopi* (R. Mena, 23 February 1993).
38. *Orellana*, Aguarico, **Campamento Chiruisla**, Área de Amortiguamiento del Parque Nacional Yasuní (0°37′S, 75°53′W): *Marmosops bishopi* (A. Molina, G. Toscano, A. Camacho, 10 November 2009).
39. *Orellana*, Aguarico, Parque Nacional Yasuní, Río Tiputini, **Comunidad Guiyero**, Bosque de Nambay [0°36′35″ S, 76°27′52″ W, 237 m; Albuja and Arguero, 2011]: *Marmosops bishopi* (L. Albuja, and A. Arguero, 19 May 2012). This locality was originally reported in the UTM coordinate system by Albuja and Arguero (2011: 30).
40. *Orellana*, Parque Nacional Yasuní, **Estación Científica Yasuní** (0°40′38″S, 76°24′05″W): *Marmosops bishopi* (A. Pérez, 4 May 2011).
41. *Pastaza*, Arajuno, área operación AGIP, Bloque 10. Comunidad de Paparahua. Cercanías **R**ío Villano (1°29′S, 77°25′W): *Marmosops bishopi* (C. Boada, 26 June 2012).
42. *Pastaza*, Arajuno, Curaray, área operación AGIP, Bloque 10, cercanías **R**ío Lliquino (including "Helipuerto K4" at 1°28′S, 77°29′W; and "Helipuerto K10" at 1°28′, 77°31′W): *Marmosops bishopi* (C. Boada, 2–18 February 2012 and 11 October 2012).
43. *Pastaza*, Arajuno, Curaray, área operación AGIP, Bloque 10. Comunidad de Tarangaro, Cercanías **R**ío Manderocayu (1°24′02″S, 77°22′59″W): *Marmosops bishopi* (C. Boada, 22–24 August 2012, and 5 November 2012).
44. *Sucumbíos*, Cantón Shushufindi, Parroquia Pañacocha, **R**ío Pañayaku [0°21′S, 76°25′W, 230 m; Tirira, 2012]: *Marmosops bishopi* (collector not recorded, 28 February 2014).
45. *Sucumbíos*, **El Reventador** [0°02′S, 77°31′W, Google Earth at "El Reventador"]: *Marmosops bishopi* (collector and date not recorded).

FRENCH GUIANA (FRANCE)

46. **Les Nouragues** [4°05′N, 52°40′W, 210 m; Voss and Emmons, 1996]: *Marmosops parvidens* (F. Catzeflis, 3 August 2002) and *M. pinheiroi* (J.-F. Mauffrey, 15 May 1999).
47. **Paracou** [5°17′N, 52°55′W, ca. 45 m; Simmons and Voss, 1998], near Sinnamary: *Marmosops parvidens* and *M. pinheiroi* (L.H. Emmons, R.W. Kays, D.P. Lunde, and R.S. Voss, 1991–1994).

48. **River Arataye** (4°00′N, 52°40′W, 30 m): *Marmosops parvidens* (L.H. Emmons, 2 October 1984).

GUYANA

49. *Cuyuni-Mazaruni,* **Mount Roraima** (including "Second Camp" at 5°17′N, 60°45′W, 800 m; and "Third Camp" at 5°16′N, 60°44′W, 1000 m): *Marmosops pakaraimae* (B.K. Lim and D.M. Jafferally, 26 February–8 March 2003).
50. *Demerara-Mahaica,* **Hyde Park**, 30 mi [up the] Demerara R[iver] [6°30′N, 58°16′W, ca. 100 m; Stephens and Traylor, 1985]: *Marmosops parvidens* (S.B. Warren, 8 September 1906).
51. *Potaro-Siparuni,* Iwokrama Forest, **Canopy Walkway** (4°15′N, 58°55′W, 70 m): *Marmosops pinheiroi* (B.K. Lim et al., 19 August 2008).
52. *Potaro-Siparuni,* Iwokrama Forest, **Kabukalli Landing** (4°17′N, 58°31′W): *Marmosops pinheiroi* (B.K. Lim et al., 13–18 October 1999).
53. *Potaro-Siparuni,* Iwokrama Forest, Turtle Mountain, **10 km NW Kurupukari** (4°44′N, 58°43′W, 50 m): *Marmosops pinheiroi* (B.K. Lim et al., 31 October 1997).
54. *Potaro-Siparuni,* **Mount Ayanganna**, First Plateau Camp (5°20′N, 59°57′W, 1100 m; Lim et al., 2010): *Marmosops pakaraimae* (B.K. Lim, 27 October 2002).
55. *Potaro-Siparuni,* **Mount Wokomung**, First Plateau Camp (5°07′N, 59°49′W, 1130 m): *Marmosops pakaraimae* (B.K. Lim and W.P. Kilburn, 19–20 February 2003).
56. *Upper Takutu–Upper Essequibo,* **Karanambo** [3°45′N, 59°18′W; Lim et al., 2008]: *Marmosops parvidens* (M.D. Engstrom et al., 1 October 1990).

PANAMA

57. *Darién*, **Cana** (= Santa Cruz de Cana [7°47′N, 77°42′W; Fairchild and Handley, 1966], 2000 ft): *Marmosops invictus* (E.A. Goldman, 14–20 March 1912).
58. *Darién*, **Cerro Tacarcuna** ([8°10′N, 77°18′W; Fairchild and Handley, 1966], 4800 ft): *Marmosops invictus* (C.O. Handley, Jr., 5–11 March 1964).
59. *Darién*, **Tacarcuna Casita Camp** ([8°01′N, 77°22′W; Fairchild and Handley, 1966], 2700 ft): *Marmosops invictus* (C.O. Handley, Jr., 21 January 1959).
60. *Darién*, **Tacarcuna Laguna Camp** ([8°04′N, 77°19′W; Fairchild and Handley, 1966], 4000 ft): *Marmosops invictus* (C.O. Handley, Jr., 9–11 March 1959).
61. *Panamá,* **Cerro Azul** [9°14′N, 79°21′W, 850–3200 ft; Fairchild and Handley, 1966]: *Marmosops invictus* (C.O. Handley, Jr., 3 February 1958).

PERU

62. *Amazonas*, Condorcanqui, Nieva, **Puerto Tunduza** [4°46′55″S, 77°52′32″W; Ruelas and Pacheco, 2015]: *Marmosops bishopi* (L. Luna, 8 November 1997; E. Vivar, 9–16 November 1997).
63. *Cusco,* Cosñipata, **Hacienda Villa Carmen** [ca. 12°50′S, 71°15′W, 600 m; Stephens and Traylor, 1983]: *Marmosops bishopi* (C. Kalinowski, 20 September 1954).
64. *Cusco*, Distrito Echarate, La Convención, Camisea, **Konkariari** ([11°48′S, 72°52′W; Velazco and Simmons, 2011], 450 m): *Marmosops bishopi* (J.L. Mena, 27 October 1997).
65. *Huánuco,* Montealegre, **Puerto Márquez** [= San Márquez at 9°32′S, 74°56′W, ca. 100 m; Stephens and Traylor, 1983], Río Pachitea: *Marmosops bishopi* (G. Tessman, 16 November 1923).
66. *Junín,* **22 mi E Tarma** ([ca. 11°25′S, 75°23′W], 7000–7600 ft): *Marmosops juninensis* (A.L. Tuttle, 21–24 June 1964; E.L. Bush, 19 June 1964).
67. *Junín,* Provincia Satipo, Distrito Pampa Hermosa, **San Antonio**, near to Río Pampa Hermosa [11°24′S, 74°46′W, 1387–1406 m; Peralta and Pacheco, 2014]: *Marmosops juninensis* (M.C. Peralta, 5–8 July 2011).
68. *Junín,* **Utcuyacu** ([ca. 11°12′S, 75°28′W; Stephens and Traylor, 1983], 1463 m): *Marmosops juninensis* (H. Watkins, 25 November 1929).
69. *Loreto,* 25 km S Iquitos, **Estación Biológica Allpahuayo** [3°58′S, 73°25′W; Hice and Velazco, 2012]: *Marmosops bishopi* (C.L. Hice, 11 October 1997–10 November 1998). This locality is equivalent to the "Reserva Nacional Allpahuayo-Mishana," which is said to be located 28 km SW of Iquitos on the Iquitos-Nauta highway (Hice and Velazco, 2012: 3).
70. *Loreto,* **Jenaro Herrera** [4°55′S, 73°40′W; Voss and Fleck, 2011]: *Marmosops bishopi* (D.P. Lunde, 6 June 2003; J.A. Amanzo, 14–20 March 1997, 13 June–3 July 2003; M. Villalobos, 9 June–27 July 2003).
71. *Loreto*, Maynas, **Alto Nanay**, Quebrada Agua Negra ([2°55′26″S, 74°49′01″W; Hurtado et al., 2014], 177 m): *Marmosops bishopi* (L. Huamaní, 25 October 2008).
72. *Loreto*, Maynas, San Juan Bautista, **Trece de Febrero,** km 31.5 carretera Iquitos-Nauta, Estación de Campo UNAP ([3°59′59″S, 73°26′31″W; Hurtado et al., 2014], 120 m): *Marmosops bishopi* (W. Sánchez, 22 April 2004).

73. *Loreto,* **Nuevo San Juan** [5°15′S, 73°10′W; Voss and Fleck, 2011]: *Marmosops bishopi* (R.S. Voss, 28 May 1998).
74. *Loreto,* **San Jacinto** [2°19′S, 75°52′W, 180 m; Duellman and Mendelson, 1995]: *Marmosops bishopi* (R.M. Timm, 4 July 1993).
75. *Loreto*, San Juan Bautista, **El Triunfo,** km 48 (including km 49) carretera Iquitos-Nauta ([4°09′02″S, 73°28′03″W; Hurtado et al., 2014], 120 m): *Marmosops bishopi* (W. Sánchez, 24 February 2004, 01 April 2005).
76. *Loreto*, San Juan Bautista, **La Habana,** km 52 carretera Iquitos-Nauta ([4°10′52″S 73°28′52″W; Hurtado et al., 2014], 120 m): *Marmosops bishopi* (W. Sánchez, 28 June 2004).
77. *Loreto*, San Juan Bautista, **San Lucas,** km 44 carretera Iquitos-Nauta, 1 km E del camino ([ca. 4°06′15″S, 73°27′48″W; Hurtado et al., 2014], 120 m): *Marmosops bishopi* (W. Sánchez, 4 February 2005). Coordinates here provided (obtained from Hurtado et al., 2014) were taken at "San Lucas km 43 carretera Iquitos-Nauta."
78. *Loreto,* **San Pedro** ("hills 0.5 to 1 km E and NE of San Pedro") [4°20′S, 73°12′W; Valqui, 2001]: *Marmosops bishopi* (M. Valqui, 20 May 1994).
79. *Loreto,* **Teniente López** (including "1½ km N of Teniente López") [2°36′S, 76°07′W, 200 m; Duellman and Mendelson, 1995]: *Marmosops bishopi* (N. Woodman, 25 July 1993; R.M. Timm, 26 July 1991).
80. *Loreto*, Tigre, margen izquierda del río Pucacuro, **Collpa Salvador** [2°37′55″S, 75°08′39″W; Watsa et al., 2012]: *Marmosops bishopi* (L. Arias, 10 July 2001).
81. *Loreto*, Tigre, Río Pucacuro (including "margen derecha" and "margen izquierda"), **Cocha Coconilla** [2°42′17″S, 75°05′50″W; Watsa et al., 2012]: *Marmosops bishopi* (L. Arias; 19 July–5 August 2001).
82. *Madre de Dios,* Albergue Lodge, **Cuzco Amazónico** [12°33′S, 69°03′W, 200 m; Woodman et al., 1991] (including "ca. 12 km E Puerto Maldonado, Río Madre de Dios"): *Marmosops bishopi* (J.E. Cadle, 8 March 1984; V. Pacheco, 18 June 1989; R. Arana, 21 January 1990).
83. *Madre de Dios*, Manu, **Blanquillo** [12°25′37″S, 70°42′17″W, 273 m; S. Solari personal commun.]: *Marmosops bishopi* (S. Solari, 11 March 1993).
84. *Madre de Dios*, Quebrada Aguas Calientes, **2.75 km E Shintuya** ([12°41′S, 71°15′W; Patterson et al., 2006], 450–520 m): *Marmosops bishopi* (B.D. Patterson, 10 September 1999; S. Solari, 30 August 1999 and 11 September 1999).
85. *Madre de Dios*, Tambopata, **R**ío La Torre [coordinates not located]: *Marmosops bishopi* (C. Ascorra, 11 December 1995).
86. *Madre de Dios*, Tambopata, S.N. **Pampas del Heath**, P.C. Enahuipa (12°39′45″S, 68°57′30″W): *Marmosops bishopi* (A. Cornejo, 19 June 1996).
87. *Pasco,* **Santa Cruz** [10°37′S, 75°22′W, 2050 m; Cadena et al., 2007], ca. 9 km SSE Oxapampa: *Marmosops juninensis* (T. Schulenberg, S. Allen, D. Stotz; 24 February 1982).
88. *San Martín*, Rioja, Pardo Miguel, Naranjos, **Caserio El Diamante** (5°45′12″S, 77°31′34″W, 1078 m): *Marmosops bishopi* (P.M. Velazco, 16–17 May 2011).
89. *Ucayali*, Contamana, Sierra de Contamana, Cerros de Canchaguaya, **Aguas Calientes** ([07°11′20″S, 74°56′54″W; Hurtado et al., 2014] 320 m): *Marmosops bishopi* (U. Paredes, 15–20 November 2000).

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90. *Brokopondo,* **Brownsberg Nature Park**, Jeep Trail (4°56′N, 55°12′W, 500 m): *Marmosops parvidens* (M.D. Engstrom et al., 13–19 April 2002).
91. *Brokopondo,* **Finisanti** [5°08′N, 55°29′W; Voss, 1991], Saramacca River: *Marmosops pinheiroi* (P. Hershkovitz, 31 December 1961).
92. *Nickerie,* **Kayser Gebergte Airstrip**, E of Zuid River [ca. 3°07′N, 56°27′W, ca. 278 m; Stephens and Traylor, 1985]: *Marmosops parvidens* (H.A. Beatty, 30 December 1960).
93. *Nickerie,* **Sipaliwini Airstrip** (2°02′N, 56°08′W): *Marmosops pinheiroi* (S.L. Williams, 20 August 1979).
94. *Sipaliwini,* **Bakhuis Transect 9** (4°29′N, 57°02′W, 170 m): *Marmosops pinheiroi* (B.K. Lim and S.L. Peters, 3 November 2005).
95. *Sipaliwini,* **Bakhuis Transect 13** (4°33′N, 57°04′W, 175 m): *Marmosops parvidens* (B.K. Lim and A.V. Borisenko, 19 January 2006).

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96. *Tobago,* **near Charlotteville** [11°19′N, 60°33′W; Voss, 1991]: *Marmosops carri* (M.E. Holden, 18–22 January 1989).
97. *Trinidad,* **Caparo** [10°27′N, 61°20′W; USBGN, 1955]: *Marmosops carri* (F.M. Chapman, 19 March–17 April 1894).
98. *Trinidad,* **Cedros** [ca. 10°06′N, 61°48′W; Goodwin and Greenhall, 1961]: *Marmosops carri* (Trinidad Regional Virus Laboratory [TRVL] collectors, 7 March 1972).

99. *Trinidad,* **Cumaca** [10°42′N, 61°09′W; USBGN, 1955]: *Marmosops carri* (W.G. Downs, 20 July 1954).
100. *Trinidad,* Sangre Grande, **Rio Grande Forest** [ca. 10°41′N, 61°01′W, 200 ft; see note]: *Marmosops carri* (W.G. Downs, 21 June–19 July 1956). Note: coordinates estimated from those of Sangre Grande (USBGN, 1955) based on Goodwin and Greenhall's (1961: 296) statement that Rio Grande Forest is ca. 10 airline miles NE Sangre Grande.
101. *Trinidad,* **St. Augustine** [10°39′N, 61°24′W; USBGN, 1955]: *Marmosops carri* (E. Friend, 2 October 1936).
102. *Trinidad,* **Turure Forest** [ca. 10°32′N, 61°07′W; Goodwin and Greenhall, 1961]: *Marmosops carri* (TRVL collectors, 1966–1969).

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103. *Aragua*, **Rancho Grande** [10°21′N, 67°40′W, ca 1000 m; Handley, 1976]: *Marmosops carri* (W. Beebe, 29 June 1946; C.O. Handley and D.J. Rhymer, 27–31 March 1960). According to García et al. (2014: 721), *Marmosops ojastii* has also been taken at this locality.
104. *Bolívar,* **85 km SSE El Dorado**, Km 121 [= "Km 125" at 6°02′N, 61°22′W, 1032 m; Gardner, 2008]: *Marmosops pakaraimae* (M.D. Tuttle, 9 May 1966).
105. *Bolívar,* **Auyán-tepui** [ca. 5°55′N, 62°32′W; Paynter, 1982], 460 m: *Marmosops pinheiroi* (G.H.H. Tate, 9 March 1938). See Voss et al. (2013) for additional information about this locality.
106. *Bolívar,* **Churi-tepui** [ca. 5°13′N, 61°54′W; McDiarmid and Donnelly, 2005], Camp 5 (4900 ft): *Marmosops pakaraimae* (E. McGuire, 13 January 1953).
107. *Carabobo,* **Cumbre de Valencia** [ca. 10°20′N, 68°00′W, 1700 m; Paynter, 1982]: *Marmosops carri* (M.A. Carriker, Jr., 20 October 1910).
108. *Carabobo,* La Copa, **4 km NW Montalbán** ([ca. 10°09′N, 68°21′W; Handley, 1976], 1513 m): *Marmosops carri* (A.L. Tuttle, 2–8 August 1968).
109. *Carabobo/Falcón/Yaracuy,* **19 km NW Urama** [ca. 10°37′N, 68°24′W, 25–60 m; Handley, 1976]: *Marmosops ojastii* (M.D. Tuttle, 19 October 1965).
110. *Distrito Federal,* 4 km N. Caracas, **Los Venados** (including locality 5 km N. Caracas [10°32′N, 66°54′W; Handley, 1976], 1443–1500 m): *Marmosops carri* (M.D. Tuttle, 10–11 August 1965).
111. *Falcón,* **near La Pastora** (including sublocalities 5 km N and 13 km E Mirimire, and 14 km ENE Mirimire; 11°12′N, 68°37′W, 122–125 m): *Marmosops fuscatus* (Smithsonian Venezuelan Project [SVP] team, 11–16 November 1967).
112. *Falcón,* **Serranía de San Luís**, Parque Nacional J.C. Falcón (including sublocalities in Sector Cerro Galícia, 10 km W and 4 km N Cabure [11°11′N, 69°42′W, ca. 1300 m; Anderson et al., 2012]; and in Sector Cumbres de Uria, ca. 9 km N Cabure [11°14′N, 69°37′W, 1320–1370 m; Anderson et al., 2012]): *Marmosops fuscatus* (J. Ochoa-G., 25 April 2006; R.P. Anderson, 12 August 2006).
113. *Mérida,* **La Azulita** [8°43′N, 71°27′S, 1135 m; Paynter, 1982]: *Marmosops fuscatus* (W.H. Osgood and H.B. Conover, 21 April 1920).
114. *Mérida,* **Mérida** (including sublocality "Rio Abbaregas" [ca. 8°36′N, 71°08′W; Paynter, 1982], 1600–1630 m): *Marmosops fuscatus* (S. Briceño, 1896–1902).
115. *Miranda/Vargas,* 9.4 km N Caracas, **Hotel Humboldt** ([10°33′N, 66°52′W; Handley, 1976], 2103–2230 m): *Marmosops carri* (M.D. Tuttle, 7 August–4 September 1965). Anderson and Gutiérrez (2009: 85) noted that SVP collections labeled "Hotel Humboldt" could have been collected either in the states of Miranda or Vargas contra Handley (1976: 79), who placed this locality on the border between the Distrito Federal and Miranda. One specimen from this locality (USNM 370035) has a recorded elevation of 1281 m, which we assume to be a lapsus for 2181 m.
116. *Monagas,* **San Augustín** (including sublocalities "2 km N and 4 km W Caripe" and "5 km NW Caripe"; 10°12′N, 63°32′W, 1150–1338 m): *Marmosops carri* (Smithsonian Venezuelan Project, 6 July 1967).
117. *Trujillo,* Hacienda Misisí, **13–14 km E Trujillo** ([9°21′N, 70°18′W; Handley, 1976], 2000–2210 m): *Marmosops carri* (SVP team, 28 January 1966; J.A.W. Kirsch, 21 June 1969).
118. *Zulia,* Pueblo Nuevo, **La Fría** [8°55′N, 71°25′W; DMA, 1993]: *Marmosops* sp. (H.B. Baker, 13 August 1914).